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BEHAVIOUR AND SOCIAL ORGANIZATION IN A POPULATION OF BLUE GROUSE ON VANCOUVER ISLAND

by

© MARTIN K. MCNICHOLL

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Behaviour and Social Organization in a Population of Blue Grouse on Vancouver Island submitted by Martin K. McNicholl in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Behaviour and social organization of male Blue Grouse were studied in a population on Vancouver Island from 1971 to 1974.

Six basic postures plus variants of each are categorized and the context of each posture and variant discussed. These postures are compared with those described in previous literature.

Males approached playbacks of all conspecific calls in Full Display, then assumed postures appropriate to the sex on seeing a dummy grouse. Birds were able to distinguish sex by plumage alone, but female calls were stronger stimuli than male plumage. The Squat posture of females was a strong releaser of courtship activity, and colourful lateral apteria comprised a strong male releaser. White shoulder-spots caused males to attack males, but repelled them from mating with females. When dummies of both sexes were presented with an accompanying call, males interacted with that of the sex corresponding to the call. Reactions to calls showed a marked seasonal pattern, varying with the particular call.

Hooting appears to be true song, functioning in both courtship and territorial contexts. Singing peaks about the time females and yearlings arrive on the study area, and diminishes towards the end of the nesting season. Daily singing patterns were similar to those shown by passerines in north temperate regions. Male Blue Grouse sing in social groups, possibly involving dominance.

Males were able to distinguish songs of neighbours in the correct direction from those of other males. Responses to stranger playbacks and total response levels were higher while responses to neighbour playbacks were lower using Stranger-Neighbour-Stranger sequences compared with Neighbour-Stranger-Neighbour sequences.

Territory size varied widely and was not obviously related to any one extrinsic parameter. Once established, the territory of a given male rarely changed, but successors did not occupy areas identical to those of predecessors. There was a strong tendency to sing from a few specific sites within the territory.

The social system of male Blue Grouse appears to combine elements of lek and solitarily territorial systems. Factors favouring such a combination of systems are discussed.

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INTRODUCTION

Blue Grouse (Dendragapus obscurus) on Vancouver Island, British Columbia have been studied almost continuously since 1950 (Zwickel and Bendell 1972; Zwickel et al. 1977). The overall objective has been to identify factor(s) responsible for regulating populations. The failure of these studies to determine a close relationship between population size and extrinsic environmental factors (Zwickel and Bendell 1972) has led to a recent emphasis on the potential importance of such intrinsic factors as social behavior (Bendell and Elliott 1967; Mossop 1971; Hemus 1972; Zwickel et al. 1977) and genetics (Redfield et al. 1972; Zwickel et al. 1977) in regulating numbers.

An understanding of social systems seems essential to an understanding of the role of behavior in the regulation of populations. The study of social organization requires information on both the dispersion of individuals and their behavior during encounters (Crook 1965; Hartzler 1972).

Male Blue Grouse on Vancouver Island are territorial (Bendell and Elliott 1967), a form of social behavior often suspected of regulating populations (Brown 1969; Watson and Moss 1970; Klomp 1972; Watson 1973; Wilson 1975). Furthermore, male Blue Grouse have a number of distinctive display features and a song (the "hoot") which they sing frequently during the breeding season (Bendell and Elliott 1967; Stirling and Bendell 1970). Thus, one might predict that territories of male Blue Grouse are maintained in the same manner as those of many passerines, that is, primarily at a distance through vocalization, and secondarily through agonistic encounters at close range (Dorst 1971).

The present study was directed toward understanding the social organization of male Blue Grouse through studying behavioral interactions among and dispersion of individuals. A proper understanding of the role of behavior in regulating Blue Grouse numbers is dependent upon such knowledge of the social behavior of the species. The thesis addresses this background information without considering population regulation. This work is presented in five papers:

1. Postures and displays of male Blue Grouse.
2. Functional aspects of some display components of male Blue Grouse.
3. Vocal communication among male Blue Grouse.
4. Neighbor-stranger discrimination by song in male Blue Grouse.
5. Territories of male Blue Grouse on Vancouver Island.

The first two papers describe and identify functions of displays and display components, the visual or close range aspects of social behavior. The first is a description of postures and displays with the context in which these occur. The second describes experimental manipulations used to differentiate reactions between males from those given by a male to a female or to a potential predator, and to identify messages conveyed by display components.

The third and fourth papers examine communication by song among territorial males through both observations and experiments. In the third, I examine daily and seasonal patterns of song and the influence of one bird's singing on that of its neighbors. The fourth presents a study of types of information conveyed by singing.

The final paper includes an examination of the size and structure of territories of male Blue Grouse on the study area, and consistency of use of territory by the same male in different years, and by successive males in the same territory site.

The results presented in these five papers are integrated into a final discussion which outlines the social system among male Blue Grouse.

LITERATURE CITED

BENDELL, J.F., & P.W. ELLIOTT. 1967. Behaviour and the regulation of numbers in Blue Grouse. Can. Wildlife Serv. Rept. Ser. No. 4.

BROWN, J.L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81:293-329.

CROOK, J.H. 1965. The adaptive significance of avian social organization. Symp. Zool. Soc. London 14:181-218.

DORST, J. 1971. The life of birds. Vol. 1. New York, Columbia Univ. Press.

HARTZLER, J.E. 1972. An analysis of Sage Grouse lek behavior. Ph.D. Thesis, Missoula, Univ. Montana.

HEMUS, H.D. 1972. A behavioural and demographic comparison of three Blue Grouse populations released on Moresby Island. B.S. (HONS) Thesis, Victoria, Univ. Victoria.

KLOMP, H. 1972. Regulation of the size of bird populations by means of territorial behaviour. Neth. J. Zool. 22:456-488.

MOSSOP, D.H. 1971. A relation between aggressive behaviour and population dynamics in Blue Grouse. M.S. Thesis, Vancouver, Univ. Brit. Columbia.

REDFIELD, J.A., F.C. ZWICKEL, J.F. BENDELL, & A.T. BERGERUD. 1972. Temporal and spatial patterns of allele and genotype frequencies at the _Ng_ locus in Blue Grouse (_Dendragapus obscurus_). Can. J.

Zool. 50:1657-1662.

STIRLING, I., & J.F. BENDELL. 1970. The reproductive behaviour of Blue Grouse. Syesis 3:161-171.

WATSON, A. 1973. A review of population dynamics in birds. Brit. Birds 66:417-437.

WATSON, A., & R. MOSS. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. pp. 167-218 _in_ WATSON, A. (Editor). Animal populations in relation to their food resources. Oxford & Edinburgh, Blackwell.

WILSON, E.O. 1975. Sociobiology / the new synthesis. Cambridge, Mass., Harvard Univ. Press.

ZWICKEL, F.C., & J.F. BENDELL. 1972. Blue Grouse, habitat and populations. Proc. Intern. Ornithol. Congress 15:150-169.

ZWICKEL, F.C., J.A. REDFIELD, & J. KRISTENSEN. 1977. Demography, behavior and genetics of a colonizing population of Blue Grouse. Can. J. Zool. 55:1948-1957.

PAPER 1: POSTURES AND DISPLAYS OF MALE BLUE GROUSE

Abstract. Postures of male Blue Grouse are categorized as six basic types and their variations. The context in which each posture type and its variants occur is documented, and accompanying sounds are discussed. Postures recorded are compared with descriptions in the literature.

During the spring and summer of 1971 to 1974, I studied the behavior of male Blue Grouse (*Dendragapus obscurus fuliginosus*) at Comox Burn (Zwickel and Bendell 1972) on Vancouver Island, British Columbia. A major portion of this study consisted of a functional analysis of certain display components, the results of which are presented elsewhere (McNicholl 1978a). As background to this analysis, I described all postures I observed while male Blue Grouse were interacting with other Blue Grouse or with an observer, or were apparently unaware of my presence. In this paper, I classify these postures into six main types with variants of each, and document conditions under which each occurred and what sounds, if any, accompanied specific postures. Previous descriptions of behavior of male Blue Grouse during the breeding season (Brooks 1926; Hjorth 1970; Stirling and Bendell 1970) concentrate primarily on displays, with postures described incidently as part of these displays. These descriptions and summaries of them in more general works (Bent 1932; Johnsgard 1973) lack consistency in terminology, and are thus difficult to compare with each other. Thus, the objectives of this paper are to provide a classification of postures that can serve as a basis for describing displays and additional postures and to compare previously published descriptions of these postures.

Study Area and Methods

The main study area was a portion of Comox Burn, described by Zwickel (1972). This area is approximately 19 km northwest of Courtenay, British Columbia. Comox Burn is characterized by low undulating ridges, running roughly parallel from east to west and intersected with stream beds and bogs. Zwickel (1972) indicated that most of the area was "very open" and "open" by the classification of Bendell and Elliott (1967) between 1969 and 1971, with limited portions classified as "dense" by late 1971. The birds I studied occupied primarily "very open" and "open" areas in 1971 and 1972; by 1973 the "very open" habitat had declined sharply with "dense" habitat markedly increasing in both 1973 and 1974. Further details of the specific territories where I studied grouse are given in McNicholl (1978b). A few notes from surrounding areas are also included.

In 1971 and 1972 my approach was observational for which relatively open habitat was an asset. The denser habitat in 1973 and 1974 hampered observation in non-experimental situations. Thus, more emphasis was placed on collection of experimental data with speakers and dummies being placed where I could readily see approaching grouse. The denser habitat in these latter years also facilitated my hiding, and thus reduced the possibility of reaction to me.

Observations on which descriptions are based were made during chance encounters, deliberate approaches, and at sites with experimental playbacks and/or models to which the bird was attracted. When males were "hooting" (singing), I was usually able to observe them from a hidden location from which I also made observations during playback experiments. Topography and vegetation was such that I could usually remain hidden without a blind, but when this was not possible, I used a brown poncho-style raincoat as a blind. Notes were taken on reactions to observers during chance encounters of any male on the study area or elsewhere, and when I approached birds to read bands after completing other observations or experiments.

Most birds studied had been previously colour-banded and were identified individually if possible. Observations and experiments were concentrated on a few individuals, approximately 20 each year, but experimental results were routinely checked on males not included among those usually studied. This approach allowed me to consider individual variation in the compilation of results, and to ensure that habituation was not responsible for waning of responses to certain experiments.

More details on manipulation of sounds and dummies during the experiments are described in McNicholl (1978a).

Results

In this paper emphasis is placed on descriptions of postures assumed and the context in which each occurs. In order to facilitate discussion of the context of these postures, a short preliminary section describes vocal and mechanical sounds produced by male Blue Grouse.

VOCAL AND MECHANICAL SOUNDS

Table I lists types of sounds I heard produced by male Blue Grouse, with associated postures and references to these sounds in the literature. These sounds are briefly described below.

Hooting

A series of five to seven (usually six) low notes, termed "hooting" by Stirling and Bendell (1970) and other authors, was the most frequently heard vocalization produced by male Blue Grouse. Hooting is treated in detail as the song of this species in a separate paper (McNicholl 1978c).

Whoot

The "whoot" was always uttered only by males courting live or dummy hens, and no reference mentions its occurrence in other situations in the field. However, Cooper (1977) reported that caged birds sometimes gave this call or another like it in aggressive situations.

Stirling and Bendell (1970) and Hjorth (1970) both provide graphical illustrations of this call, showing the double-note characteristic of the "whoot."

My earliest record of the "whoot" is 22 March 1974, the day the first female Blue Grouse was seen on Comox Burn that year (John Kristensen, pers. comm.), but I did not hear "whoots" again until 9 May. My earliest dates for 1972 and 1973 were 11 May and 7 May respectively, roughly corresponding to start of laying on Vancouver Island in some years (Zwickel 1965), but later than early laying in other years (last week of April, Zwickel 1977). Zwickel (pers. comm.) has several late April records. Peak occurrences of "whoots" appear to be in May and June (Table II), but they were occasionally heard as late as 5 August (1972). The data in Table II are only rough estimates of seasonal occurrence, as the call was heard much more frequently during crepuscular periods than during mid-day. However, as all times of day except during the dark of night were sampled in all months in at least one year of the work, these data should serve as an approximation of the seasonality of "whoots."

Growl

Male Blue Grouse give a call which Bendell and Elliott (1967) described as a series of short stacatto phrases like the growling of a dog (Canis familiaris), and thus termed it the "growl." Both Stirling and Bendell (1970) and Hjorth (1970) show sonograms of this call. Other descriptions of this call are given in Table I, and situations when I heard it are also summarized in Table I.

Mechanical Sounds

In 1928 C. de B. Green (quoted in Bent 1932: 99) described a flight display of D. o. richardsonii, which has been described in more detail by Blackford (1958) and for D. o. pallidus by Wing (1946). These displays appear to constitute an important component of the behavioral repertoire of at least some inland races (Hjorth 1970; Johnsgard 1973; Harju 1974), but in D. o. fuliginosus, this display is much reduced (Bendell and Elliott 1967; Stirling and Bendell 1970). I heard a slightly prolonged flutter only twice, and could see the associated activity neither time, although in both cases a male and a female grouse were in the vicinity.

I did, however, note a "loud landing" which may be a reduced version of this aerial behavior, on 105 occasions outlined in Table I. At least some of these sounds may have been aerial but my impression was that they were all made on or just prior to landing. F.C. Zwickel (pers. comm.) watched a male "flutter flight" down a ridge in three or four flights in response to the playback of a recording of a female call.

POSTURES AND DISPLAYS

"Posture" is defined for birds by Thomson (1964) as "the pose in which the body is held." In this paper, I describe each posture I saw, even those seen only rarely. Context in which each posture occurred is significance and signal value of each posture. I use "display" in the sense of Armstrong (1947) and Hinde (1964) as visual signalling, which may or may not be accompanied by sound, rather than the sense of Smith (1969) in which the sound (especially song) may be considered a display itself.

Neutral Posture

The Neutral Posture (Fig. 1), as used here and by Cooper (1977) essentially lacks display features. While in the Neutral Posture the bird is in a stance neither horizontally nor vertically exaggerated. The crest is down and combs are inconspicuous, occasionally showing yellow under prolonged observation, but never extended. The neck is neither stretched nor withdrawn and the "lateral apteria" (Hjorth 1970; referred to as "air sacs" by most early authors, such as Brooks 1926, as "gular sacs" by Johnsgard 1973, and as "nuchal sacs" by Salt and Salt 1976) are not visible. The ring of white feathers around the lateral apteria is not visible unless the bird is walking, when it is barely evident as a thin line. The "white shoulder-spot" (Lumsden 1970) is also hidden. The wings are held against the body and not drooped. As most of my observations were made after a bird was aware of me or various other stimuli, or while it was singing, I rarely observed this posture. In only 13 cases did I observe this posture before the bird detected my presence. In 24 other cases confiding individuals retained this posture when I came into view, although sometimes moving a short distance away. On one occasion, an approachable bird assumed this pose after initially responding to my approach by Crouching. Equivalent postures described in the literature are included in Table III.

Crouch Posture

In the Crouch Posture (Fig. 2, and Cooper 1977: Fig. 1d), the bird remains flattened against the ground (or, in heavily forested areas, on a limb - Bent 1932: 110); the crest and combs are down, neck withdrawn, lateral apteria invisible and white feathers surrounding them rarely showing, wings pressed against the body with no indication of the white shoulder-spot, and tail pressed to the ground. While in the Crouch Posture, a bird usually remains motionless, although it occasionally turns its head or blinks. Vocalizations rarely accompany this posture (Table IV), with only 2 of 153 observations including sound. One bird uttered a "growl" once on one encounter and five times on another. This posture was adopted in response to my approach.

I observed three variations of the Crouch Posture (Table III). The Crouch, Head Up Posture was identical to the Crouch except that the head was raised, and in one instance the crest was also raised. This posture was assumed under the same circumstances as the Crouch on 13 occasions, and was derived from the Crouch on two others (Table IV). The Semi-Crouch was also identical to the Crouch except that the bird remained standing, with legs partially bent at the tibiotarsal-metatarsal joint. The horizontal stance of the body and tail differentiates this posture from the Neutral Posture and the lack of extension in the neck differentiates it from the Horizontal Aggressive Posture. The Semi-Crouch was derived from the Crouch on four occasions, and was the initial reaction to the observer on four others. The Mobile Crouch was exactly like the Semi-Crouch except that the bird walked instead of remaining still. On ten of the 14 occasions in which I observed the Mobile Crouch, the bird assumed this posture as an initial reaction to me.

Table IV documents behaviour of birds immediately after 153 observations of the Crouch or one of its variants.

Alert Posture

The typical Alert Posture is illustrated by Bendell and Elliott (1967: Fig. 5a). In this posture, the grouse is characterised by a raised tail (Mossop 1971). The body is held as in the Neutral Posture, with crest elevated, combs not extended and frequently but not always coloured (Table V). The neck is slightly stretched and the lateral apteria only rarely visible, although the white feathers surrounding them are sometimes slightly evident as a thin white line (Table V). Wings are held to the side and not drooped, with no indication of the "white shoulder-spot". The tail is elevated but not fanned. The bird is normally silent, but on 11 (of 114) occasions "growled" at me.

In addition to the basic Alert Posture, I observed nine variations of it. Table V indicates comb colouration and visibility of white feathers around the lateral apteria for each, as well as the number of occasions on which "growls" were given by birds in each. No other calls accompanied any of these postures. The most commonly observed variation was the Alert, Tail Down Posture (Fig. 3) which was identical to the Alert, except that the tail was not elevated. The Alert, Crest Down Posture was also identical to the Alert except that the crest was not raised (Fig. 4). In the Partial Alert Posture, both tail and crest were down. This differs from the "standing tall" aggressive posture of Stirling and Bendell (1970) in lacking the exaggerated vertical stance, and from the Neutral Posture in the slightly stretched neck. The "white shoulder-spot" was displayed in four variations of the Alert Posture: Alert Plus White Shoulder-Spot; Alert, Tail Down Plus White Shoulder-

Spot; Alert, Crest Down Plus White Shoulder-Spot; and Partial Alert Plus White Shoulder-Spot postures; all grouped under Alert Plus White Shoulder-Spot in Tables V and VI. These were identical to the postures of the corresponding names except for the addition of the "white shoulder-spot" and outward opening of the wings necessary to display the shoulder-spot.

On two occasions male Blue Grouse assumed the Alert Plus Apteria Posture, in which the lateral apteria were exposed, and on three occasions the Alert, Tail Down Plus Apteria Posture, identical to the Alert, Tail Down Posture except for the addition of the exposed lateral apteria. A growl accompanied the latter posture on one of the three occurrences, but no sounds accompanied the former. Table VI shows that Alert Postures of various types were adopted most frequently in response to me, and less often by a bird trespassing on the territory of another when the trespassor saw a live or dummy male Blue Grouse. Table VII indicates behavior before and after the various Alert postures.

Hooting Posture

I base my description of Hooting Posture (Fig. 5) on 508 observations of male Blue Grouse hooting before the bird was aware of my presence and in the absence of apparent stimuli from other grouse, except hooting on other territories. As noted by Edson (1925), the body is held at an angle of approximately 45° with the head nodding up and down towards the breast with each syllable (Stirling and Bendell 1970), resulting in the head being held forward by a somewhat curved neck. The crest is down and the combs not extended and showing no color or only a trace of yellow. The oesophageal pouch is inflated (Hjorth 1970), causing the neck to swell, thus resembling the display postures of certain pigeons (Columbidae) (Johnson 1929). The beak opens and closes with the initiation of each stanza of hooting. The lateral apteria are not visible, but the white feathers surrounding them often show as a thin line, showing briefly as flashes with each syllable. The wings are held to the sides with no evidence of the white shoulder-spot. The tail is not fanned, and is held slightly below or above the horizontal, being raised and lowered with each syllable (Hjorth 1970; Fig. 40). In all cases, "hooting," accompanied this posture except very briefly if a bird paused when I came into view.

A male in the Hooting Posture would immediately and invariably assume the Hooting With Exposed Apteria variant of the Hooting Posture on first sighting me (Fig. 6). All males which reacted to me by remaining and continuing to hoot, did so at least initially in this posture, and those which flushed or walked away assumed this posture at least briefly prior to leaving. The Hooting With Exposed Apteria Posture is identical to the Hooting Posture except that the lateral apteria are partially or completely exposed, and thus the ring of white feathers which surrounds each apterium is visible.

Harju (1974) noted that the "gular sacs" (= lateral apteria) are oval while hooting and round while "strutting," but the shape depends on how wide the feathers surrounding the apterium are opened, and may vary considerably during a single observation, a finding confirmed by D.A. Boag (pers. comm.).

Full Display Posture

In the Full Display Posture, the male's body is approximately horizontal, with the crest down, combs fully extended and yellow, orange or red, neck neither elongated nor withdrawn, lateral apteria fully exposed with surrounding white feathers fully displayed, wings partially drooped to the side with no indication of the white shoulder-spot, and tail fanned and raised slightly over the body, but not tilted to one side. Birds did not usually hoot in this posture, instead assuming the Hooting in Full Display variant of it, but I noted six instances in which a bird remained in the Full Display Posture while hooting. One male "growled" at me while in Full Display. Whenever a male Blue Grouse approached a male or female dummy and/or a playback recording of either sex, he exhibited the Full Display Posture. In addition, Full Display was assumed in response to me 58 times, and once to a truck. Although this is essentially a walking and standing posture, eight birds displayed extended combs and exposed apteria during flight, two flying in to approach playbacks of hooting, four flying towards female calls, and two flying away from me after having responded to dummies.

I observed nine variations of Full Display (Table III). Males approaching live or dummy females assumed the Full Display Plus Tail-Tilt Posture. Here, males tended to be more upright than in Full Display, with one wing fully open and the tail tilted to the side opposite the open wing. This posture was assumed only in response to live or dummy females: female calls alone were not sufficient to induce it. Grouse apparently remained silent while in this posture, but in the "rush and whoot" and "head bob" postures of Stirling and Bendell (1970), which usually follow the Full Display Plus Tail-Tilt, the "whoot" is given.

Two rarely observed variations of Full Display were the Full Display with Unfanned, Raised Tail and Full Display with Crest Up postures, both identical to Full Display with the exception of the features implied in their names. The former was observed six times, the latter three times, all occurrences in response to me. No sounds were heard when either of these postures was adopted.

The Full Display With White Shoulder-Spot Posture was identical to Full Display except that the bird's wings were opened and tilted to show the white shoulder-spot, which is otherwise hidden. This posture was once assumed in response to me, but usually occurred during experiments involving female calls and strong male features (including lateral apteria) or white shoulder-spots as visual features on an accompanying female dummy. A variation of this posture observed only once was the Full Display With Tail-Tilt and White Shoulder-Spot Posture, assumed during an experiment with a female call and female dummy with artificial apteria attached.

Partial Display is essentially a less intense version of Full Display in which the lateral apteria are only partially exposed, the combs not raised, and the tail up but not fully fanned (Blackford 1963: Fig 7). I observed this posture, apparently in response to me (28 times), when approaching a taped recording of hooting within the territory (five times), and approaching female calls (three times). In addition, this posture was assumed frequently after playback recordings or dummy experiments had been terminated and during neighbor-stranger discrimination experiments (Falls and McNicholl in press). Birds which assumed Full Display in response to playbacks of either male or female calls usually approached the recording in Partial Display, then assumed Full Display on nearing the source of the sound. During neighbor-stranger discrimination experiments, birds at their hooting sites initially would assume Full Display briefly before leaving the hooting site, then assume

Partial Display en route, and finally resume Full Display close to the speaker. Occasional hooting en route often accompanied Partial Display. Two variations of Partial Display, both apparently assumed in response to me, were seen. Both are identical to Partial Display except for the features described in their names: Partial Display With Crest Up and Partial Display With Crest Up and Tail Down.

In the Hooting in Full Display Posture, the bird's body is elevated at about a 45° angle, with crest down but combs extended and coloured in shades ranging from bright yellow through orange to brilliant red, neck normal in length but swollen in appearance, lateral apteria and surrounding white feathers fully exposed, wings to the side and somewhat drooped, with no white shoulder-spot, and tail fanned and raised, but only to about a 45° angle and thus not over the back. Hooting with Exposed Apteria differs from this posture in that the tail is not up and fanned, the wings are held to the sides, and the combs not flared. Hooting in Full Display was assumed by all birds approaching dummies or recordings of either sex while in the Full Display Posture, and especially while walking around the speaker when recordings were played in the absence of dummies. The bird would approach in Full Display, stop and assume the Hooting in Full Display Posture, hoot, then revert to Full Display as described by Hjorth (1970), but with the occasional exception noted above. Hooting in Full Display was also assumed in response to me on 27 occasions.

Copulation Postures

During mounting and copulation, male Blue Grouse undergo a series of postures described briefly by Bendell and Elliott (1967) and in more detail by Stirling and Bendell (1970) and by Hjorth (1970). In attempted copulations with dummies, the basic sequence of events I observed was essentially as described and illustrated by Hjorth (1970: Fig. 51). Since these postures are described well and readily equated between authors, I shall not described them further here, but regard them as additional variations of Full Display. One feature not mentioned by either Hjorth (1970) or Stirling and Bendell (1970), but illustrated by both is the elevation of the rump feathers during copulation.

Aggressive Postures

I observed five postures assumed by territorial male Blue Grouse, presumably in response to live or dummy male Blue Grouse, that were followed by attack in the case of dummies and fleeing by intruding birds. Thus, I refer to these postures as aggressive.

The most commonly observed was the Aggressive, Tail Down Posture in which the bird is standing with the feathers pressed tightly to his body (Fig. 7). The crest is down, but combs are extended and colored yellow through red. The neck is stretched with no sign of the lateral apteria or feathers surrounding them. The wings are held to the sides of the body, not drooped, and with no indication of the white shoulder-spot. The tail is down. On 10 of 15 occasions, I heard birds in this posture "growl." I recorded birds assuming this posture in response to playback of hooting without dummies on seven occasions, to male dummies on five occasions, and to the observer three times.

An identical variant except that the tail was up and partially fanned (Fig. 8) was observed on seven occasions, five times in response to a male dummy and twice to a live male. I termed this the Agressive, Tail-Up Posture. No sounds were heard on any of the seven occasions observed.

Three additional aggressive postures included white shoulder-spots. The Aggressive, Tail Down Plus White Shoulder-Spot Posture was identical to the Aggressive, Tail Down Posture except that the wings were opened in such a manner as to show the white shoulder-spot. I described this posture as assumed in response to male dummies four times and to live males twice. This variant was accompanied by a "growl" on four occasions (15 "growls" on one of these). I once observed the Aggressive, Tail-Up Plus White Shoulder-Spot, identical to the Aggressive, Tail-Up Posture except for the addition of the shoulder-spot and wing movements necessary to achieve this. This posture was assumed in response to a male dummy, and was accompanied by a "growl." On one occasion, I observed the Horizontal Aggressive Plus White Shoulder-Spot Posture, in which the body was held horizontally, with crest down, combs extended and red, neck stretched, lateral apteria and surrounding white feathers not showing, wings open and tilted forward to show the white shoulder-spot but not drooped, and tail horizontal. It was assumed in response to a male dummy and was accompanied by "growling."

Discussion

In this discussion, I first compare my classification with terminology in the literature, as summarized in Tables I and III. The motivation, significance and signal value of each posture and sound are then considered, followed by a brief discussion of the problem of conflicting motivation and its manifestation, and consideration of the biological significance of the variations of each basic posture.

COMPARISON WITH THE LITERATURE

Vocal and Mechanical Sounds

Hooting is discussed in detail in another paper (McNicholl 1978c), and therefore not considered further here.

The "whoot" was referred to as "oops!" by Brooks (1926) and Blackford (1958), both of whom appeared to regard it as a single note. Brooks (1926) studied D. o. pallidus for which Hjorth's (1970) sonograms clearly show two notes, a point he emphasized. I prefer the term "whoot" to "single hoot" used by Hjorth (1970), since the call consists of two notes, neither of which is identical to a single hoot. However the similarity of the words "hoot" and "whoot" may be a source of confusion in conversations regarding these sounds.

Although I have treated the "growl" as one call here, there is a strong possibility that the "gugugugug" and "ca-ca" descriptions of this call (Table I) refer to two distinct, though similar calls, as also suggested by Cooper (1977). As noted by Blackford (1963) the "alert" note given as an intruder approached can be barely audible, and I found the "gugugugug" phrasing appropriate in such circumstances. Calls given to other males, however, seem much harsher, and better described by the "ca-ca" phraseology.

Flutter flights and loud landings may be different, or loud landings may be greatly reduced forms of the flutter flight in D. o. fuliginosus. I suspect that loud landings are derived from flutter flights, but constitute a distinct behaviour pattern. Zwickel's observation quoted above seems to me a distinctly different behaviour than the loud landings I observed. This points needs clarification, however, as even the two workers most familiar with this population (J.F. Bendell and F.C. Zwickel) disagree as to whether these are distinct sounds or not (pers. comm.).

Postures

The Neutral Posture has been referred to by others under similar names, and does not offer a source of confusion (Table III). Cooper (1977) describes a "rest posture" and several maintenance postures not included in this paper.

Similarly other descriptions of the Crouch Posture are not sources of confusion. The Semi-Crouch Posture does not appear to have been described previously, although Skinner (1927) may have been referring to this posture when he stated that Blue Grouse "freeze in their tracks." The Mobile Crouch appears to be identical to Mossop's (1971) "Crouch and run," except that the birds ran on only two of the 14 occasions when I observed it, and one bird ran only briefly after walking slowly. The birds walked slowly throughout the other 12 observations. The term Crouch as used in these postures should not be confused with Brook's (1926) "crouching position," which referred to a stage of Full Display during courtship of a hen. In Blue Grouse, males are on their toes throughout courtship, but in some grouse, the males are actually crouched down on the whole feet during part of the courtship display, invoking such terms as "Crouching cum Head-Jerking" for Franklin's Spruce Grouse (Canachites canadensis canadensis), "Crouched Forward" for Okhotsian Grouse (Falcipennis falcipennis), "Forward cum Crouching" in the Black Grouse (Lyrurus tetrix), and "Confronted Crouching" in the Greater Prairie Chicken (Tympanuchus cupido), Lesser Pinnated Grouse (T. pallidicinctus) and Sharp-tailed Grouse (Pedioecetes phasianellus) (Hjorth 1970), and "crouching" by a male Rock Ptarmigan (Lagopus mutus) "attempting to induce a hen to crouch" for copulation (MacDonald 1970). Similarly, Watson (1972) has used the term "Crouched Run" and Alway (1977) "nervous crouch" for certain agonistic postures in Rock Ptarmigan and Franklin's Spruce Grouse respectively. Watson (1972), however, also used the term "crouching" in Rock Ptarmigan in the sense used here, when approached by a man.

Most of the variants described here of the Alert Posture do not appear to have been distinguished previously, and my basic Alert Posture is identical to that of others (e.g. Bendell and Elliott 1967; Mossop 1971). Lumsden (1970) did not list any of the Alert postures of male Blue Grouse as including white shoulder-spots.

The literature is somewhat contradictory on the posture assumed while hooting. The posture I term Hooting Posture was described well by Edson (1925) and both described and illustrated by Bendell and Elliott (1967: Fig. 5b) and Stirling and Bendell (1970: Fig. 2). Hjorth (1970) referred to the lack of special exhibition of "plumage or fleshy parts of the body" during "routine hooting," but did not provide a description. His "Oblique" may include it in part, but he provided no illustration. Edson (1925) also described the transition between Hooting and Hooting with Exposed Apteria postures as displayed by one male, and Stirling and Bendell (1970) also mention this transition, but without referring to the specific context. Hjorth (1970) referred to a gradual transition from the "routine hooting stance" to Full Display in response to females, but did not mention Hooting With Exposed Apteria, his Oblique cum Multiple Hoot Canto corresponding more closely to Hooting in Full Display. Bent (1932) described the Hooting with Exposed Apteria posture from his observations on one male, and contrary to my observations both Blackford (1963) and Harju (1974) imply that this posture is assumed regularly while hooting. I suspect that this variant is assumed only when the bird is aware of an observer, although subspecies differences are possible.

The literature contains a wide array of terms corresponding to the various postures I include as Full Display and its variants. Edson (1925) described Full Display without naming it on the basis of one male, and Brooks (1926) referred to it briefly as the "crouching" position at the beginning of courtship. Cooper (1977) illustrated the posture as "feather spread," a term also used by Stirling and Bendell (1970: Fig. 4). However, the wing is more drooped in their figure than described here or shown by Cooper. Hjorth (1970) described this as the "display walking" position, although I include stationary birds in Full Display, and the tail is slightly less forward than in Hjorth (1970: Fig. 45). The Full Display Plus Tail-Tilt Posture constitutes the courting displays described by Brooks (1926), Skinner (1927), and Blackford (1958), and corresponds to the "full courting display" described by Bendell and Elliott (1967) and shown in their figure 5d. Hjorth (1970) described this as "Upright cum Tail-Tilting." Lumsden (1970) cited S.D. MacDonald as observing the white shoulder-spot as shown by one male D. o. richardsonii during courtship display. Otherwise, the Full Display with White Shoulder-Spot does not appear to have been described previously. The Hooting in Full Display Posture corresponds to Hjorth's (1970) "Oblique cum Multiple Hoot Canto." Johnsgard (1973), citing Hjorth's description, incorrectly implies that this is the posture usually assumed by males during hooting. I doubt that this posture is ever assumed in the absence of stimuli from other grouse or observers within or immediately adjacent to the territory, except perhaps in response to loud female calls on an adjacent territory.

The Aggressive, Tail-Down Posture corresponds to the "standing tall" posture of Stirling and Bendell (1970), but is not described by others. The Aggressive Tail-Up Posture corresponds to the posture shown by Hjorth (1970: Fig. 52a), except that the birds were more sleek than shown by him. As these two authorities differ on the aggressive posture shown, they appear to be contradictory as to whether the tail is up or down in the aggressive posture, whereas both are correct. The Aggressive, Tail Down Plus White Shoulder-Spot resembles the "neck stretch" posture shown by Stirling and Bendell (1970: Fig. 14), except that I did not distinguish their neck stretch and standing tall as different postures. The Aggressive, Tail-Up Plus White Shoulder-Spot Posture corresponds to the posture shown by Hjorth (1970: Fig. 53a). The Horizontal Aggressive Plus White Shoulder-Spot Posture corresponds to Bendell and Elliott's (1967) Threat Posture and Stirling and Bendell's (1970) Horizontal Posture except that neither of these include the white shoulder-spot. Lumsden (1970) cited S.D. MacDonald as noting the white shoulder-spot on male D. o. richardsonii during attacks on mirror images, and Stirling and Bendell (1970) drew attention to the white spot in the caption to their figure 14 depicting the "neck stretch," but did not discuss it.

MOTIVATION, SIGNIFICANCE AND SIGNAL VALUE OF POSTURES AND SOUNDS

Vocal and Mechanical Sounds

Male Blue Grouse "hoot" when approaching intruders of either sex on territory (McNicholl 1978a). This suggests that hooting is important both in expelling male intruders and in courting hens. Additional evidence indicates that hooting is the song of Blue Grouse, as discussed in detail elsewhere (McNicholl 1978c).

Whoots were always uttered prior to mounting during the courtship behaviour of males at hen dummies (McNicholl 1978a) in the "Rush cum Single Hoot Call" sequence of Hjorth (1970). All sequences of behaviour in non-experimental situations in which I heard a male give the "whoot" also involved live hens. Thus, I agree with previous authors that this is a courtship call (Brooks 1926; Hjorth 1970; Stirling and Bendell 1970). However, this call or one very similar was given in aggressive situations in captivity (Cooper 1977), so that an aggressive function is also possible. Until such time as the latter situation is observed in the field, however, I believe it best to regard Cooper's observations as the result of the highly artificial situation of birds kept in small cages.

Growls were given both in aggressive situations and during interactions with me (Table I). No growl was given in the three instances when birds assumed one of the aggressive postures in my presence, but growls were uttered during other interactions with me. In these cases the growls were of the less harsh type ("gugugugug"). In contrast, growls given during aggressive encounters were of the harsher ("ca-ca") type. Thus, the softer type appears to convey fear or possible ambivalence in the presence of a potential predator, whereas the harsher type appears to be aggressive.

Loud landings are heard in two situations: when a territorial male is flushed and flies a very short distance from the observer, and when a territorial male is courting a hen. This suggests that loud landings are an expression of territoriality, emphasizing the presence of the resident male.

Postures

The Neutral Posture was assumed only when birds did not see me or occasionally by a few tame birds in my presence. Thus, this posture appears to be the normal stance adopted by birds not interacting with other grouse or potential predators, not engaged in any sort of maintenance activity and not singing. Cooper (1977) found that Blue Grouse isolated in cages spent more than half their time in this posture or in a "rest posture."

The Crouch is unquestionably a posture assumed in order to avoid detection by a predator. When assumed as an ititial reaction to an observer, the Semi-Crouch probably represents the immediate response of birds given insufficient warning to assume a Full Crouch. My data (Table IV) showing that most birds in the Crouch, Head Up Posture subsequently either ran away in one of the Alert postures or flew, support Cooper's (1977) suggestion that raising the head from the Crouch posture is an "intention movement" (Daanje 1951). The Mobile Crouch appears to be a strong avoidance reaction to a potential predator (my data) or, as the "Crouch and Run" to a more dominant male (Mossop 1971).

Alert Postures, like Crouches, appear to be responses to potential danger, either as a prelude to predator avoidance or just before escape from dominant or resident males. All my observations of males assuming these postures in response to live or dummy males (Table VI) were of males trespassing on territories of other males. These postures appear to be a group of "ambivalence" postures (Tinbergen 1952; Morris 1956; Hinde 1973), each representing a particular "compromise" (Andrew 1956) between tendencies to flee and to remain in the occupied place. The variety of comb color displayed, and the inclusion of the white shoulder-spot in some variations of Alert postures are consistent with this interpretation.

The Hooting Posture was never assumed in an experimental situation involving dummies or calls, agreeing with the suggestion of Bendell and Elliott (1967) and Stirling and Bendell (1970) that this posture is assumed during routine hooting only. On approach by an observer, the grouse spread feathers to partially expose the lateral apteria in an apparent "intention movement" (Daanje 1951), signalling a bird's readiness to assume Partial Display or Full Display. The Hooting with Exposed Apteria assumed as a result of this feather movement is maintained in the continued presence of an observer, but is not maintained if the observer approaches too closely. Thus, this posture appears to be a "compromise" posture (Andrew 1956) in a conflict situation of remaining to hoot vs. reacting to an observer (or predator) by fleeing, Crouching or approaching.

Responses of male Blue Grouse to playbacks show that Full Display is assumed by a resident male Blue Grouse as a reaction to any conspecific on his territory, and not primarily as a courtship posture (McNicholl 1978a). Thus, Full Display signals to the intruder that a resident male is approaching. Intruding males also assume this posture, but only near a female, and only in the absence of the resident male. Such intruders immediately assume one of the Alert postures and run away if the resident male approaches. On the other hand, Full Display With Tail-Tilt was assumed only in the presence of a live or dummy female, and is thus clearly a courtship posture. Partial Display appears to be a transitional posture between Neutral and Full Display, and also after

Full Display, when the stimulus is waning. Full Display With Crest Up, Full Display With Unfanned, Raised Tail and the two Full Display postures with white shoulder-spots all appear to be "compromise" postures (Andrew 1956) between courtship and attack or fleeing tendencies. Hooting in Full Display represents an exaggeration of Full Display in both territorial and courtship situations. This posture was assumed both before and after Full Display, and appeared to emphasize the message of Full Display. Hooting in Full Display thus fits the criteria of behavioural "punctuation" in the sense of Hailman and Dzelzhalns (1974), except that it occurs infrequently.

The Aggressive Postures appear to have been correctly interpreted as indicating aggression by Stirling and Bendell (1970), Mossop (1971), and others, as I observed these postures as assumed only in response to live or dummy males, except as rarely directed towards me.

CONFLICTING MOTIVATIONS AND THEIR MANIFESTATION

A number of variants of basic postures are clearly manifestations of conflicting motivations. These postures combine various features of different basic postures, such as Full Display features with the raised crest of Alert postures. These "compromise" postures are: all the Alert postures, Hooting With Exposed Apteria, Full Display With Crest Up, Full Display With Unfanned, Raised Tail, and the two Full Display postures which include white shoulder-spots.

The white shoulder-spot (Lumsden 1970) or white flash (Cooper 1977) occurs in various conflict situations, such as in some of the Alert postures, during aggressive interactions, and at the approach of an observer (potential predator) while the male is courting a hen. Thus, I agree with Lumsden (1970), Hjorth (1970), and Cooper (1977) that the white shoulder-spot may represent "fear" and possibly "subordinance" in conflict situations. This feature is discussed in more detail in McNicholl (1978a).

Combs often form a striking feature of male grouse (Hjorth 1970; MacDonald 1970), often remaining constant in color. In male Blue Grouse they are extended in postures connoting a high degree of "emotion;" variations of Full Display, Aggressive postures, and Alert postures. As noted by Wing (1946), Blackford (1958) and Hjorth (1970), comb color changes during displays ranging from dull yellow through bright yellow and orange to red, presumably depending on blood flow within the combs (Hjorth 1970). This color change appears to reflect intensity of reaction rather than being a reaction in itself.

SIGNIFICANCE OF VARIANTS OF BASIC POSTURES

Postures are grouped in this paper according to presumed derivation from a few basic types. Some of these variants clearly signify different motivations (e.g. Full Display vs. Full Display Plus Tail-Tilt), while others appear to be subdued or exaggerated forms of the basic posture (e.g. Partial Display vs. Full Display vs. Hooting in Full Display; Crouch vs. Semi-Crouch vs. Mobile Crouch). Several are manifestations of conflict situations. The significance of rarely observed postures needs clarification, and the possibility that some may be more prevalent at certain times of day warrants investigation, though I did not find strong indications of this. In this paper, I have attempted only to group these postures according to basic themes, and to compare postures already described in the literature with each other and with the terminology used here.

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Table I. Vocal and mechanical sounds of male Blue Grouse

Sound	Associated Behaviour	Other Terms Published
A. Vocal:		
Hoot	Singing in Hooting Posture or variant; Stop to hoot in Full Display (rarely) or Full Display Plus Tail-Tilt	Multiple Hoot - Blackford (1958); Hjorth (1970).
Whoot	In courtship: particularly in "Rush cum Sing Hoot Call" (Hjorth 1970)	Oop! - Brooks 1926; Blackford 1958 Single Hoot Call - Hjorth (1970)
Growl	To live or dummy males & taped hooting (28 records); in response to me (38 records) -possibly two calls-see text	"alert" note - Blackford 1963; "gugugugug" - Stirling and Bendell (1970); "ca-ca" - Mossop (1971); Rogers *fide* Johnsgard (1973).
B. Mechanical:		
Flutter flight	Heard only twice; activity not seen	see Blackford (1958, 1963) or Hjorth (1970) for various terms
Loud landing	Heard 3 times when male landed near playback of hen call or hen; 35 times on flushing and landing close; 67 times when Whoots also heard and both sexes present	

Table II. Number of days on which Whoots were heard, 1972-1974

Month	Number of days on which Whoots were heard
March	1
April	0
May	13
June	10
July	2
August	2

Table III. Postures, grouped as variants as six main types.

Basic Posture	Variant(s)	Published Equivalents
1. Neutral		Normal neutral pose (Mossop 1971); Neutral appearance (Hjorth 1970)
2. Crouch		other authors use same term
	a. Crouch, Head-Up	
	b. Semi-Crouch	
	c. Mobile Crouch	Crouch and Run (Mossop 1971)
3. Alert		other authors use same term
	a. Alert, Tail Down	
	b. Alert, Crest Down	
	c. Partial Alert	
	d. Alert + White Shoulder-Spot	
	e. Alert, Tail Down + White Shoulder-Spot	
	f. Alert, Crest Down + White Shoulder-Spot	
	g. Partial Alert + White Shoulder-Spot	
	h. Alert + Apteria	
	i. Alert, Tail Down + Apteria	
4. Hooting		same or similar term by others possibly Oblique of Hjorth (1970), in part.

Table III (Cont.)

Basic Posture	Variant(s)	Published Equivalents
Hooting (cont.)	a. Hooting With Exposed Apteria	not specifically named by others
5. Full Display		Crouching (Brooks 1926) Feather Spread (Stirling and Bendell 1970; Cooper 1977) Display walking (Hjorth 1970)
	a. Full Display + Tail Tilt	courting displays (Brooks 1926; Skinner 1927; Blackford 1958) Full courting display (Bendell and Elliott 1967) Upright cum Tail-Tilting (Hjorth 1970)
	b. Full Display with Unfanned, Raised Tail	
	c. Full Display with Crest Up	
	d. Full Display + White Shoulder-Spot	
	e. Full Display with Tail-Tilt + White Shoulder-Spot	
	f. Partial Display	
	g. Hooting in Full Display	Oblique cum Multiple Hoot Canto (Hjorth 1970)

Table III (Cont.)

Basic Posture	Variant(s)	Published Equivalents
6. Aggressive, Tail Down		Standing Tall (Stirling and Bendell 1970)
	a. Aggressive, Tail Up	Fighting behaviour in Fig. 52A of Hjorth (1970)
	b. Aggressive, Tail Down + White Shoulder-Spot	similar to neck stretch of Stirling and Bendell (1970)
	c. Aggressive, Tail Up + White Shoulder-Spot	Shoulder patch display in Hjorth (1970: Fig. 53A)
	d. Horizontal + White Shoulder-Spot	Similar to Threat Posture (Bendell and Elliott (1967) & Horizontal Posture (Stirling and Bendell 1970) with addition of shoulder spots.

Table IV. Number of male Blue Grouse exhibiting variations of the Crouch and other behaviour patterns after previous assumption of the Crouch or its variants

Post-Crouch Behaviour	Previous Crouch posture			
	Crouch	Crouch, Head Up	Semi-Crouch	Mobile Crouch
Remained crouched (15+ min.)	17	1	-	-
Crouch, Head Up	2	-	-	-
Semi-Crouch	4	-	-	-
Mobile Crouch	10	-	-	-
Resume Hooting Posture	4	0	1	0
Resume Neutral Posture	9	1	0	0
Show one of Full Display postures	8	1	0	0
Show one of Alert postures	62	10	2	13
Show Aggressive postures	2	0	0	0
Growl	7*	0	0	0
Flush	[illegible]	2	5	0
Total	153	15	8	13

* on two occasions while still in Crouch

Table V. Number of male Blue Grouse showing comb colour and white feathers surrounding lateral apteria and "growling" during Alert postures

	Combs		White Feathers		Growl	
	colour shown*	colour not shown	slightly visible	not shown	yes	no
Alert	32	82	4	110	11	103
Alert, Tail Down	15	42	1	56	8	49
Alert, Crest Down	9	25	0	34	1	33
Partial Alert	6	5	2	9	0	11
Alert Plus White Shoulder-Spot'	1	6	0	7	0	7
Alert Plus Apteria	2	0	2	0	0	2
Alert, Tail Down Plus Apteria	3	0	3	0	1	2

* Red in two instances of Alert Posture; yellow in all others

' 4 postures combined; Alert Plus White Shoulder-Spot Posture; Alert, Crest Down Plus White Shoulder-Spot Posture; Alert, Tail Down Plus White Shoulder-Spot Posture; Partial Alert Plus White Shoulder-Spot Posture

Table VI. Number of male Blue Grouse that reacted to three stimuli by assuming Alert postures

Posture	Observer	Other live or dummy male	Chick Whistle
Alert	111	5	1
Alert, Tail Down	54	2	0
Alert, Crest Down	32	3	0
Partial Alert	11	0	0
Alert Plus White Shoulder-Spot*	7	0	0
Alert Plus Apteria	2	0	0
Alert, Tail Down Plus Apteria	3	0	0

* Combining four postures as in Table V.

Table VII. Number of male Blue Grouse that assumed various behaviour patterns before and after assuming Alert postures

Behaviour pattern	Before	After
Hooting or standing quiet	123	109
Crouch	87	87
Flush	14	31
Full Display or variant	3	1
Aggressive	1	0

Fig. 1. Neutral Posture of male Blue Grouse

Fig. 2. Crouch Posture of male Blue Grouse.

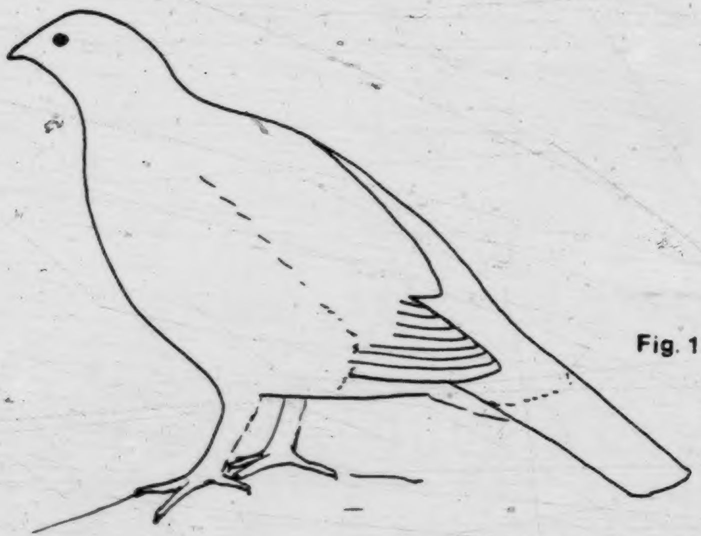

Fig. 1

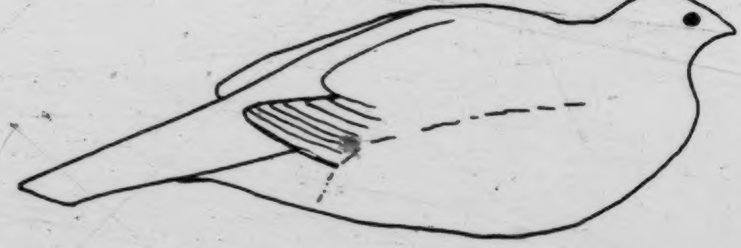

Fig. 2

Fig. 3. Alert, Tail Down Posture of male Blue Grouse.

Fig. 4. Alert, Crest Down Posture of male Blue Grouse.

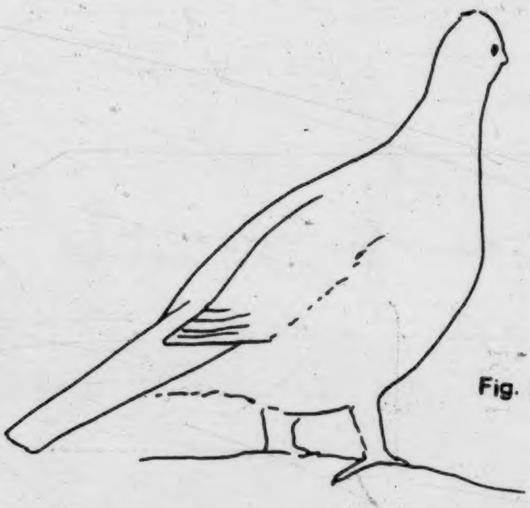

Fig. 3

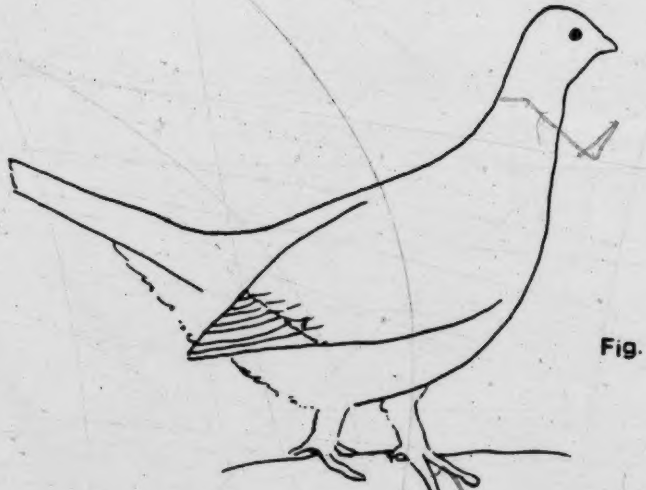

Fig. 4

Fig. 5. Hooting Posture of male Blue Grouse.

Fig. 6. Hooting with Exposed Apteria Posture of male Blue Grouse.

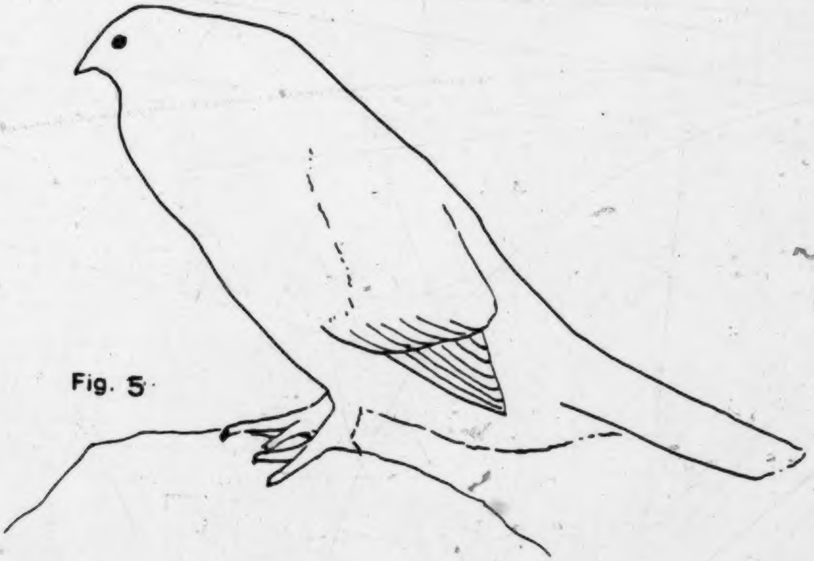

Fig. 5

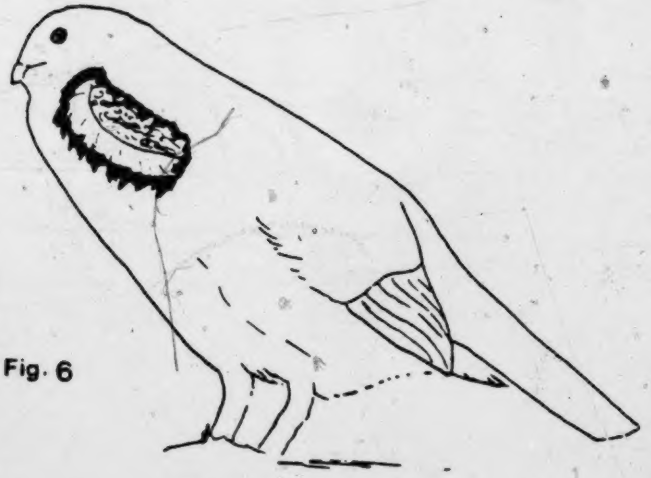

Fig. 6

Fig. 7. Aggressive, Tail-Down Posture of male Blue Grouse.

Fig. 8. Aggressive, Tail-Up Posture of male Blue Grouse.

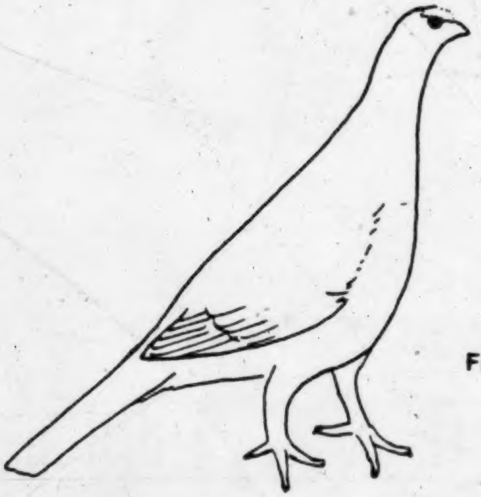

Fig. 7

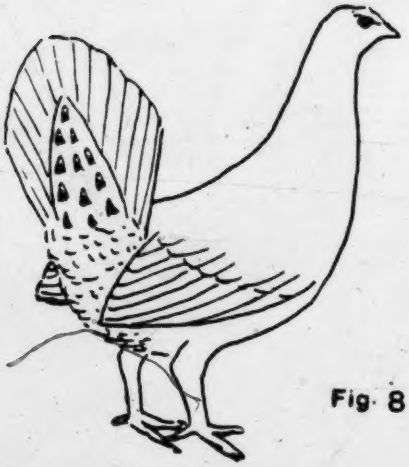

Fig. 8

REFERENCES

Alway, J.H. 1977. A study of social behaviour relating to brood breakup and dispersal in Franklin's Grouse (Canachites canadensis franklinii) under captive conditions. M.Sc. thesis, Edmonton: University of Alberta.

Andrew, R.J. 1956. Some remarks on behaviour in conflict situations. British J. Anim. Behav., 4, 41-45.

Armstrong, E.A. 1947. Bird display and behaviour: an introduction to the study of bird psychology. Second ed. New York: Dover.

Bendell, J.F., and P.W. Elliott. 1967. Behaviour and the regulation of numbers in Blue Grouse. Can. Wildlife Serv. Rept. Ser., No. 4.

Bent, A.C. 1932. Life histories of North American gallinacious birds. U.S. Natl. Mus. Bull., 126.

Blackford, J.L. 1958. Territoriality and breeding behavior of a population of Blue Grouse in Montana. Condor, 60, 145-158.

Blackford, J.L. 1963. Further observations on the breeding behavior of a Blue Grouse population in Montana. Condor, 65, 485-513.

Brooks, A.C. 1926. The display of Richardson's Grouse, with some notes on the species and subspecies of the genus Dendragapus. Auk, 43, 281-287.

Cooper, C.R. 1977. Differences in behaviour between populations of captive Blue Grouse. M.Sc. thesis, Toronto: University of Toronto.

Daanje, A. 1951. On locomotory movements in birds and the intention movements derived from them. Behaviour, 3, 48-98.

Edson, J.M. 1925. The hooters of Skyline Ridge. Condor, 27, 226-229.

Falls, J.B., and M.K. McNicholl. in press. Neighbor-stranger discrimination by song in male Blue Grouse. Can. J. Zool.

Hailman, J.D., and J.J.I. Dzelzkalns. 1974. Mallard tail-wagging: punctuation for animal communication? Amer. Nat., 108, 236-238.

Harju, H.D. 1974. An analysis of some aspects of the ecology of Dusky Grouse. Ph.D. thesis, Laramie: University of Wyoming.

Hinde, R.A. 1964. Display. pp. 202-205 in Thomson, A.L. (editor). A new dictionary of birds. New York: McGraw-Hill.

Hinde, R.A. 1973. Behavior. pp. 480-535 in Farner, D.S. and J.R. King (editors). Avian Biology. Vol. 3. New York: Academic Press.

Hjorth, I. 1970. Reproductive behaviour in Tetraonidae with special reference to males. Viltrevy, 7, 184-588.

Johnsgard, P.A. 1973. Grouse and quails of North America. Lincoln: University of Nebraska Press.

Johnson, R.A. 1929. Summer notes on the Sooty Grouse of Mount Rainier. Auk, 46, 291-293.

Lumsden, H.G. 1970. The shoulder-spot display of grouse. Living Bird, 9, 65-74.

MacDonald, S.D. 1970. The breeding behavior of the Rock Ptarmigan. Living Bird, 9, 195-238.

McNicholl, M.K. 1978a. Functional aspects of some display components of male Blue Grouse. in Ph.D. thesis, Edmonton: University of Alberta.

McNicholl, M.K. 1978b. Territories of male Blue Grouse on Vancouver Island. in Ph.D. thesis, Edmonton: University of Alberta.

McNicholl, M.K. 1978c. Vocal communication among male Blue Grouse. in Ph.D. thesis, Edmonton: University of Alberta.

Morris, D. 1956. The feather postures of birds and the problem of the origin of social signals. Behaviour, 9, 75-113.

Mossop, D.H. 1971. A relation between aggressive behaviour and population dynamics in Blue Grouse. M.Sc. thesis, Vancouver: University of British Columbia.

Salt, W.R., and J.R. Salt. 1976. The birds of Alberta. Edmonton: Hurtig.

Skinner, M.P. 1927. Richardson's Grouse in the Yellowstone Park. Wilson Bull., 39, 208-214.

Smith, W.J. 1969. Messages of vertebrate communication. Science, 165, 145-150.

Stirling, I., and J.F. Bendell. 1970. The reproductive behaviour of Blue Grouse. Syesis, 3, 161-171.

Thomson, A.L. 1964. A new dictionary of birds. New York: McGraw-Hill.

Tinbergen, N. 1952. "Derived" activities; their causation, biological significance, origin and emancipation during evolution. Quart. Rev. Biol., 27, 1-32.

Watson, A. 1972. The behaviour of the Ptarmigan. British Birds, 65, 6-26, 93-117.

Wing, L. 1946. Drumming flight in the Blue Grouse and courtship characters of the Tetraonidae. Condor, 48, 154-157.

Zwickel, F.C. 1965. Early mortality and the numbers of Blue Grouse. Ph.D. thesis, Vancouver: University of British Columbia.

Zwickel, F.C. 1972. Removal and repopulation of Blue Grouse in an increasing population. J. Wildl. Manage., 36, 1141-1152.

Zwickel, F.C. 1977. Local variation in the time of breeding of female Blue Grouse. Condor, 79, 185-191.

Zwickel, F.C., and J.F. Bendell. 1972. Blue Grouse, habitat and populations. Proc. Internatl. Ornithol. Congr., 15, 150-169.

PAPER 2. FUNCTIONAL ASPECTS OF SOME DISPLAY COMPONENTS OF MALE BLUE GROUSE

Although displays of male Blue Grouse (Dendragapus obscurus) have been described in detail by several authors (Brooks 1926; Hjorth 1970; Stirling and Bendell 1970; and others), an experimental analysis of the functions of display components is lacking.

From 1971 to 1974, I studied the social behavior of male Blue Grouse on Vancouver Island, British Columbia. Part of the study consisted of an analysis of functions of some display components in males. This study was designed to differentiate general displays from displays or postures assumed in response to only males or females, or to intruding observers (presumed to be equivalent to predators).

METHODS

This study was conducted on Comox Burn (Zwickel and Bendell 1972), approximately 19 km northwest of Courtenay, British Columbia. The general area is described by Zwickel (1972) and Martin (1973), and specific territories of grouse which I studied are described by McNicholl (1978a).

I conducted experiments to test the reactions of male Blue Grouse to vocal and visual stimuli within their territories. The primary objective was to determine which display feature(s) males might use in repelling another male from his territory and/or for challenging a resident on the latter's territory. However, displays and display features (including song) frequently have more than one function (Lack 1940, 1974; Armstrong 1947, 1973; Andrew 1956, 1961; Hinde 1964; and others). Therefore, to distinguish features or displays which signal agonistic intentions to another male from those used as a general response to all grouse or to females only, the experimental repertoire included models and taped vocalizations of both sexes. A priori assumptions based on previously published work (e.g. Hoffman 1956; Blackford 1958, 1963; Boag 1966; Bendell and Elliott 1967; Harju 1974; and others) were that males are territorial and promiscuous, or at least not monogamous, and will thus court any female entering their territories.

The male call I used for playback was the song, generally known as Hooting (Stirling and Bendell 1970). This song is common and readily recorded in the field. For a female call, I initially selected the Whinny, so termed by Stirling and Bendell (1966). This call had been recorded in an aviary when females were in precopulatory situations. However, some males did not respond to this call by approach when they would actively court or chase females and/or would approach calls of young chicks or imitations of these. Thus, I tested reactions of males to other female calls also. I chose a cluck given by hens when with chicks (hereafter the Brood Cluck), partly because it often elicits a response from males at times when they do not react to the Whinny. I also used the Liquid Cluck (Kristensen 1973), a call I had recorded when a hen gave it on finding a dummy hen at her nest.

To determine reactions of males to the presence of each sex on their territories, I used mounted specimens with strong male characters and others with strong female characters in test situations. I chose a male in Full Display posture in which conspicuous male characters are displayed (McNicholl 1978b), and a female in the Squat posture (Stirling and Bendell 1970: Fig. 9), assumed by females before and during copulation. When presented to live birds, I anticipated that these dummies should elicit the most extreme responses to males and females respecively, especially if accompanied by appropriate calls. To determine the most extreme response by one male to another male on his territory, I presented him with a Full Display male dummy while playing taped Hooting. For the most extreme response to a female, I presented him with a Squat female dummy accompanied by taped Whinny, Brood Cluck or Liquid Cluck. To differentiate between the opposite reactions I anticipated from these experiments, I also presented males with intermediate dummies: a male in a posture identical to Full Display but with no exposure of lateral apteria or white feathers surrounding them; a male mounted in the female Squat posture; a female mounted in Full Display, including false lateral apteria; and a female mounted in Full Display, but lacking lateral apteria. Each of these postures was presented to males with and without accompany-ing playbacks of both Hooting and female calls on different occasions, so that a wide range of male and female stimuli were presented. Two additional dummies were constructed by attaching white "shoulder-spots" (Lumsden 1970) to the Full Display, non-apteria mounts of each sex.

An additional experiment was designed to test the relative strengths of male and female calls when played in the presence of mounts of each sex. Mounts of both a Full Display male and a Squat female were presented together to a male while either Hooting or female calls were played.

A less rigorous experiment was to present males with an imitated call of young chicks, noting the response of the male. These experiments were presented opportunistically. The results of these experiments provide a comparison to seasonal trends in association with other stimuli.

All experiments with dummies and playbacks were preceded by a 10 min observation period during which I took notes of any vocalizations or other activity while out of sight of the bird. If playbacks were used, I started the recordings immediately after the observation period. A speaker was located near the dummy(ies) which was/were set in place in close proximity to, but out of sight of, the bird to be tested. When birds did not approach, these negative results were used in tabulations of response to calls, not in tabulating responses to dummies.

Silent dummies could not be presented without some form of observer intrusion. These were presented by one of two methods. For individuals known to be inclined to flush on seeing an observer, dummies were attached to a telescoping pole and moved into view of the subject from a concealed location. This allowed the observer to remain hidden for at least most of the experiment. In the case of more tame birds, the male was slowly driven in the direction of the dummy until he saw it, at which time I would hide while still watching him.

Approximately 20 males in each year served as principal experimental subjects, of which most (33 of 36) were previously color-banded. I attempted to remain out of sight of the bird as much as possible and in most cases confirmed the identity of the subject during the experiment. Otherwise, I identified the subject after a 10 minute observation period. Length of the experimental period depended on the reaction of the bird. If males did not react after 30 min. of playback, the experiment was terminated.

If a bird had to be identified through a deliberate approach by me, the reaction to me was recorded. These data were also noted for any accidental encounters with males.

To reduce habituation to taped calls, (Falls 1969; Krebs 1971; Verner and Milligan 1971; Petrinovich and Peeke 1973; Brooks and Falls 1975), I usually presented a particular call to a given male only once per week but in a few cases calls were played both at the beginning and at the end of the week.

The recording of the Whinny was supplied by J.F. Bendell from a call recorded in an aviary. All other calls used in playbacks were recorded in the field.

Early playbacks were done with a Uher 4000 Report L tape recorder or occasionally with a portable Sony cassette recorder, but for the majority of playback experiments, I used a Nagra 3B tape recorder with a wooden speaker column in which four oval 9 inch speakers plus a 4 inch tweeter were mounted. Each call was played on a continuous loop mounted in Cousino Audiovendor tape cartridges. These loops consisted of one call each, followed by 10 sec of silence, an interval within the normal range of Hooting intervals for this population of Blue Grouse (McNicholl 1978c). Each vocalization was played at the volume which I estimated to be normal for the particular call, as response to recordings of songs may be influenced by the volume of the playback (Brooks and Falls 1975).

RESULTS

When male Blue Grouse responded to calls of either sex, they did so in a standard manner. The initial response was to begin Hooting if they had been silent previously, first by uttering a few soft hoots, with these becoming louder. If already Hooting, the initial response was to lower the volume and alter the rate, usually Hooting at more frequent intervals when any female call was played, and matching the rate of the playback if Hooting was played. Subjects which did not approach the sound continued Hooting at the new rate as long as the tape was played. On the other hand, subjects which did approach stopped Hooting at regular intervals at the initiation of approach, but Hooted intermittently en route. Approach by territorial males to calls of either sex when played inside the boundaries of their own territories was immediate in only 8 cases of 247 positive approaches (5 to playback Hooting; 3 to playbacks of Whinny calls). In the remaining 239 approaches (96.7%), the resident did not approach until after at least five minutes, and usually longer. In contrast, nonresident males which appeared inside territories of other birds at playbacks of female calls did so very quickly, always in less than five minutes. These birds appeared to be yearlings, as they were browner and smaller than most territorial males, and in some cases band combinations proved they were either yearlings or two-year old birds not yet known to have territories. When birds approached all playbacks they appeared near the speaker in Full Display, although much of the approach was in Partial Display (McNicholl 1978a).

Responses to playbacks of Hooting within territories, summarized in Fig. 1 show that males did not respond to Hooting within their territories early in the season. As territories were large (mean 2.11 ha), and territorial males spent most of their time Hooting at a small number of spots (McNicholl 1978a), ensuring that the playback was within the territory was simple. About the time adult females and yearlings arrive (mid to late April), males responded vocally but did not approach the sound. Failure to approach the speaker was not merely an artifact of the experiment as other males, presumably yearlings or two-year olds without territories, also Hooted within territories of adult males during this period. These birds were not approached by the resident. By late April intruders and playbacks of Hooting were approached in Full Display. The transition from no approach to approach was brief: only one of 23 birds approached the speaker from 1-15 April, and only 2 of 19 from 16-25 April (1 each on the 24th and 25th), but 6 of 8 birds approached from 26-30 April. However, during the entire period intruding males, either living or mounted, when seen by resident males within their territories were always attacked, whether vocal or silent.

Figs. 2-4 summarize responses to playbacks of recorded female calls. There was a marked seasonal response to the Whinny and a possible seasonal response to other calls. There was a positive response to at least one type of female call throughout the season from mid April to the end of July, but possibly not prior to mid-April. In addition to lowering the volume and increasing the frequency of Hooting in response to calls of females, males frequently (32.4% of positive responses) omitted one or more syllables from each song.

Males sometimes flew toward playbacks of Brood Clucks. This response was highest in May (27.3% of the birds tested, N=22, vs. none in June, N=24, vs. 7.1% in July, N=14); the incidence of walking only part way towards the speaker was greatest in June (41.7% vs. 13.6% in May and 7.1% in July). From 19 to 30 June no males approached playbacks of Brood Clucks (N=10). The tendency to approach the speaker when Brood Clucks were played then increased in July.

Response to the Liquid Cluck differed from that to the other female calls in that the male never approached the speaker directly, but circled in a wide arc before approaching it closely. This suggests a ventriloqual effect of this call. I twice observed males responding to

Liquid Clucks of live hens, and on both occasions they ran around in wide circles in Full Display, apparently experiencing difficulty locating the hen. One male apparently found the hen after approximately 20 min., as I heard several Whoots (a male courtship call, Stirling and Bendell 1970), but the other male never located the hen before she moved off his territory. The stimulus which invoked this call in these two hens is unknown; no nest was in the vicinity in either case.

Table 1 documents data on reactions of male Blue Grouse to imitation chick whistles, a call given by chicks when they are separated from the hen and/or brood. These data also show a seasonal response, although this was complicated by responses of individual birds. Positive responses included pausing briefly in one of the Alert postures (McNicholl 1978a) and approaching in Full Display or a variant of Full Display.

When male Blue Grouse approached dummies, they always appeared in Full Display and were usually silent. On seeing a male dummy accompanied by a playback of Hooting, the bird assumed an Aggressive posture (McNicholl 1978b), sometimes with the white shoulder-spot, and always attacked the dummy (Table 2). On seeing a female dummy in the Squat posture, accompanied by any female calls, the subject "courted" the dummy in the behavioral sequence described by Hjorth (1970) and Stirling and Bendell (1970), and then mounted it.

In the absence of calls, all male dummies were attacked regardless of stance, whereas all females were courted (Table 2). Silent females in the Squat posture were mounted, as were those with raised tails. Males in the female Squat posture were usually attacked when silent, but courted and mounted when accompanied by female calls. "Hooting" female dummies in the Squat posture were courted and mounted, whereas "hooting" females with raised tails but no artificial apteria were attacked if silent or accompanied by Hooting, but courted if accompanied by female calls. In the latter case, courting males displayed the white shoulder-spot. Males with the white shoulder-spots were attacked by territorial males, whether silent or accompanied by calls of either sex. Females with white shoulder-spots were courted but not mounted if silent or with female calls. The subject also displayed white shoulder-spots when female calls accompanied these dummies. When females with white shoulder-spots were accompanied by Hooting, the subject assumed an Aggressive posture, but reverted to courtship behavior without mounting.

Experiments described in Table 2 were conducted with speaker and dummy close together, but in 40 experiments (20 with Hooting males and 20 with females and female calls), dummies were kept about five feet from the speaker to test whether the bird approached the sound or dummy. In all cases, the bird approached the sound only until seeing the dummy, and then approached the latter.

In 22 experiments male and female dummies were presented simultaneously. Subject males interacted with the dummy of the same sex as the playback call which accompanied the experiment, i.e. attacked male dummies when Hooting was played, and courted female dummies when Whinnies and Brood Clucks were played (Table 3).

DISCUSSION

DISPLAY COMPONENTS

In this section, I discuss the apparent signal value of certain display components, as indicated by results of experiments described above. Terminology for postures follows McNicholl (1978b).

Responses of male Blue Grouse to playbacks show that Full Display is assumed by a resident male Blue Grouse as a reaction to any conspecific on his territory, and not primarily as a courtship posture. Thus Full Display signals to the intruder that a resident male is approaching. Intruding males also assume this posture, but only near a female, and only in the absence of the resident male. Such intruders immediately assume one of the Alert postures and run away if the resident male approaches.

Experiments showing that all male dummies were attacked and all female dummies courted in the absence of calls indicate that plumage alone is sufficient for a grouse to distinguish sex. The Squat posture, however, was a powerful stimulus for mounting and courtship behavior, since male dummies in this posture were mounted if accompanied by female calls. "Hooting" by female dummies in this posture was not a sufficient male stimulus to provoke attack and override the tendency to mount birds in the Squat.

Hjorth (1970) commented that the striking effect of the fanned, raised tail in Full Display may aid in sex recognition. This hardly seems necessary if plumage alone is sufficient for such recognition. Hjorth emphasized the raised tail as an element of threat, an interpretation supported by its occurrence in some Aggressive postures (McNicholl 1978b). The fact that female dummies with raised tails inhibited mounting in all but 3 of 45 cases supports his interpretation also. On the other hand, raised tails did not prevent attacks on male dummies, and Stirling and Bendell (1970) indicated that the most extreme aggressive postures were those with the tail down.

The striking combination of the bright yellow "air sacs" (Brooks

1926; Cooper 1977; and others) and white feathers surrounding them in D. o. fuliginosus has been remarked upon by several authors (e.g. Bendell and Elliott 1967; Hjorth 1970). These "air sacs" are in fact two areas of conspicuous yellow skin on the side of the neck which are devoid of feathers and deeply furrowed. Thus, Hjorth (1970) more accurately termed them "lateral apteria." This remarkable exposure of apteria is highly suggestive of a display function, as birds usually keep apteria hidden by feathers (Stettenheim 1972). Although tail-up female dummies were courted by males (Table 2), these males attacked such dummies vigorously if artificial yellow apteria were added. Non-resident males approaching female playbacks retreated rapidly if the resident approached in Full Display, or if any form of dummy with yellow apteria was present at the speaker. These data and the fact that resident males approached all grouse dummies in Full Display suggest that exposure of the lateral apteria form a strong "social releaser" (Tinbergen 1948) in this species leading resident males to attack, causing intruding males to flee, and possibly attracting females. The white feathers surrounding these apteria were apparently not necessary to elicit these reactions. Their function is unknown, except perhaps as emphasis for the yellow apteria.

The white shoulder-spot (Lumsden 1970) or white flash (Cooper 1977) occurred in various conflict situations, such as during aggressive interactions, at the approach of an observer while the male is courting a hen, and in various Alert postures (McNicholl 1978b). These observations lead me to agree with Lumsden (1970), Hjorth (1970), and Cooper (1977) that the white shoulder-spot may represent "fear" and possibly "subordinance" in conflict situations. The fact that males will court male dummies if female calls are played, but will attack the same dummies with the same calls if artificial white shoulder-spots are added, suggests that the shoulder-spot is a strong releaser of aggression. Contrary to Hjorth's (1970) remarks that the shoulder-spot does not occur on aggressors in this species, Stirling and Bendell (1970) illustrated it on an aggressor, and I have elsewhere described three Agressive postures which include this feature (McNicholl 1978b). Aggressors which display these structures may be subordinate individuals which happen to be in the place where they are most dominant (i.e., their own territory), and thus in a conflict situation of high motivation to attack an intruding male, but "afraid" the latter may be more dominant. On the other hand, the fact that males would not mount female dummies with this feature attached (Table 2), suggests that the white shoulder-spot may inhibit males when displayed by females.

The finding that male Blue Grouse orient towards visual stimuli once they see dummies is consistent with studies on several other singing birds, indicating that birds tend to orientate towards sounds at a distance, but towards visual stimuli at close range (e.g. Stein 1963; Brooks and Falls 1975; Emlen et al. 1975; and others). When Hooting, Blue Grouse tend to orientate towards other hooting neighbors (pers. obs.), and when Hooting is played back, will turn to face the new sound (Falls and McNicholl in press).

The results of my experiments with two dummies, one of each sex, and a call of one sex only showed that subject males interacted with the same sex as the call being played. This emphasizes the powerful stimulus of calls noted in the ability of female calls to override sex identification by plumage.

These results differ from those obtained from "arena" tests by Mossop (1971), Hemus (1972), Donaldson (1973), Low (1974), and Bergerud and Hemus (1975), in which they played female calls in the presence of a female dummy and a set of mirrors. Males were attracted to the female call and the dummy, but then interacted with the mirrors. The movements of the males in the mirrors may explain the apparent contradiction in our results. In my experiments, the birds were presented with two immobile dummies and a call. In the arena experiment, the male is presented with an immobile female dummy, a call, and mobile male mirror images. The subject in the arena tests assumed an Aggressive posture towards the male in the mirror, which in turn shows an Aggressive posture. This causes the subject to show a "fear" reaction (Cooper 1977), which is also shown by the bird in the mirror. Ideally, the subject would be presented with two mobile dummies, each of which would react in a manner appropriate to a response of that sex, rather than showing behavior identical to that of the subject. I believe the variables are less confusing in my method of presenting two immobile dummies, and thus my results are more clear-cut than those obtained through mirror tests.

SEASONALITY OF RESPONSE TO PLAYBACK

Results of playback experiments showed a marked seasonality of response to grouse calls. Although males showed a positive approach to female calls from mid-April until the end of June, there was a seasonally differential response to different calls. The lack of response to the Whinny prior to mid-April correlates well with Simard's (1964) physiological data, showing adult males to be in full breeding condition from the first week of April to the first week of June. The early seasonal waning of response to taped Whinnies in comparison to other female calls is consistent with the proposal that this call is pre-copulatory (Stirling and Bendell 1966, 1970). The greatest response to the Liquid Cluck was during May and June, when hens are on nests, the location of most records of this call in the wild (Kristensen 1973). The difficulty experienced by males in locating the source of this call would be adaptive in keeping them from harassing hens at the nest, if this call is usually given there. Responses to brood clucks were strong long before broods were active, possibly indicating a more general response to clucks in general. Response to "chick whistles" was variable among males, but nevertheless tended to be strongest in June and July when chicks are most apparent.

A lack of aggressive response to Hooting early in the season does not indicate that male Blue Grouse are not yet territorial, as they attacked any live or dummy male seen on the territory at this time. Nor does this lack of response indicate that Hooting does not serve a territorial function, as believed by Harju (1974), as the later positive approach shows. The increase in response to Hooting correlates well with arrival of hens and yearlings. The short period of Hooting by numerous birds that results from lack of eviction of birds Hooting on the territory may be important in synchronizing, and possibly stimulating, breeding behavior of females. Since adult male Blue Grouse tend to be highly traditional in the use of previously established territories (McNicholl 1978a), and potential challengers (i.e. yearlings and younger adults) arrive with the females, early males would be little threat to residents. Early males on a resident's territory are most likely birds en route to other territories. On the other hand, it may be important to a male to advertise his territorial ownership by challenging and evicting any male seen on his territory.

The tendency of resident males to approach Hooting and to attack male dummies on the territory indicates that the a priori assumption that males are territorial was correct. The fact that Hooting is used in response to both male and female calls indicates that this song serves both in territorial and courtship functions. The fact that males will mount any female dummy in an appropriate posture supports the second a priori assumption that males will mate with any female within the territory.

SUMMARY

Reactions of male Blue Grouse to playbacks of Blue Grouse calls and dummies of both sexes were tested. Male Blue Grouse approached all playbacks in Full Display, then, on seeing the dummy, assumed postures appropriate to the sex. Birds were able to distinguish sex by plumage alone, but female calls were stronger stimuli than male plumage. The Squat posture of females is a strong releaser of courtship activity, and colorful lateral apteria of males comprise a strong male releaser invoking attack by residents and fleeing by intruders. White shoulder-spots caused males to attack males, but repelled them from mating with females and appears to be an indicator of conflict situations. A raised tail may be at least partly aggressive in nature. When two dummies were presented with an accompanying call, males interacted with the sex corresponding to the call.

Reactions to calls showed a marked seasonal pattern. Hooting was not approached early in the season, but was approached after females and yearlings arrived. After mid-April some female call would be approached, but each female call stimulated approach at different portions of the

season.

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Table 1. Percentage responses by male Blue Grouse to imitation "chick whistles." Sample sizes are in parenthesis.

Time Period	No response	Pause in an Alert posture	Approach in Display posture
March		100(1)	
April	20(10)	55(27)	24(12)
1-15 May	25(11)	50(22)	25(11)
16-31 May	23(10)	41(18)	36(16)
1-15 June	19(5)	12(3)	69(18)
16-30 June	0(0)	33(7)	67(14)
1-15 July	0(0)	21(4)	79(15)
16-31 July	11(3)	48(13)	41(11)
August	50(3)	33(2)	17(1)

Table 2. Responses of male Blue Grouse to models on territory.

Model	No. of trials Female calls	 Hooting	 Silent	Results
Squat female	35	20	12	court and mount in all cases
Squat male	17	13	13	with female calls court and mount; attack with Hoot; attack in 12 silent; court and mount in 1
Tail-Up Female without "apteria"	25	12	8	Court in all cases; mount in 3 with female calls
Tail-Up Male with "apteria"	20	20	10	attack all Hooting and silent dummies; court but do not mount with female calls
Full Display female	20	23	10	attack silent and Hooting dummies; with female calls court but do not mount, and show white shoulder-spot
Full Display male	30	38	10	attack all Hooting and silent dummies; attack dummies with female calls in 29 cases, court but do not mount in one case
White Shoulder-Spot female	8	10	8	court but do not mount silent dummies; with female calls court but do not mount and show white shoulder-spot; with male calls show Aggressive postures but revert to courtship without mounting
White Shoulder-Spot male	10	12	8	Territorial males attack in all cases Non-territorial males flee (5 cases)

Table 3. Reaction of male Blue Grouse to male and female dummies together.

SAMPLE SIZE	CALL PLAYED	DUMMIES	RESPONSES
10	Hooting	Squat female, Full Display male	ignore female; attack male in all cases.
12	Whinny or Brood Cluck	Squat female, Full Display male	ignore male; court and mount female in all cases.

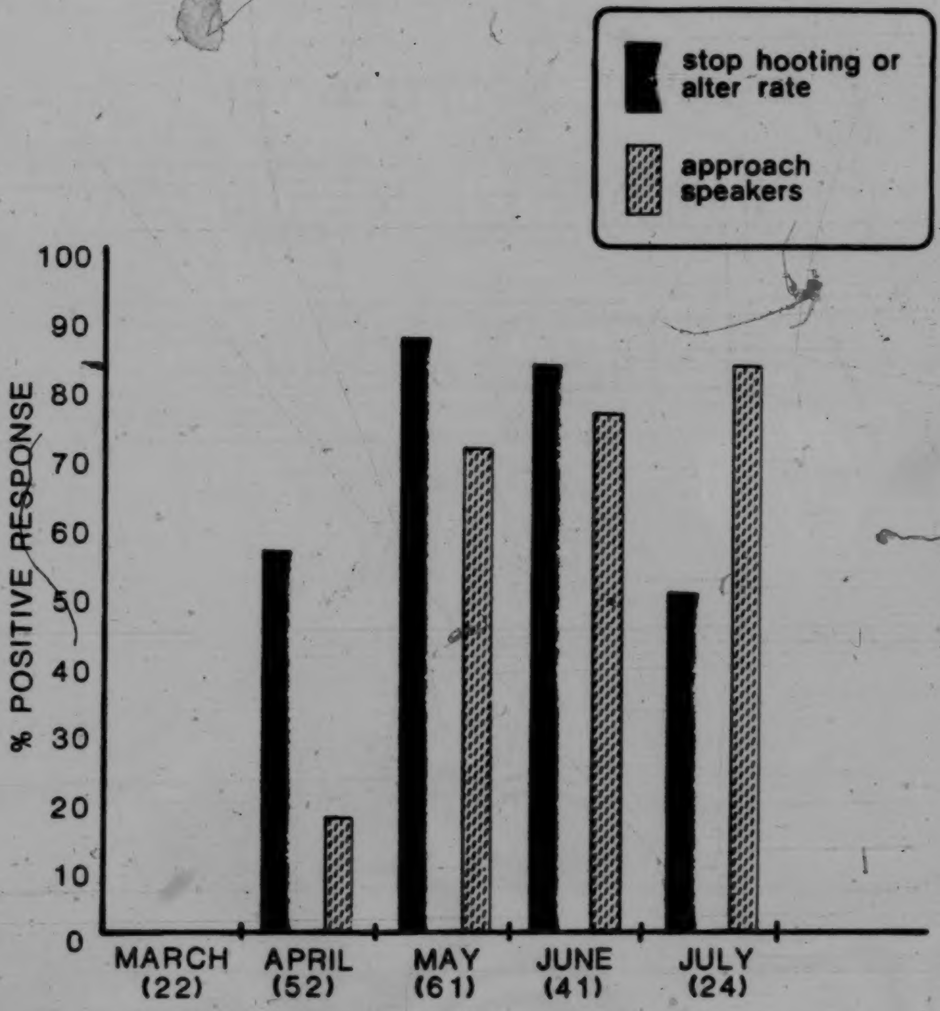

Figure 1 Response of Male Blue Grouse to Playbacks of Hooting within Territories (sample size in parentheses)

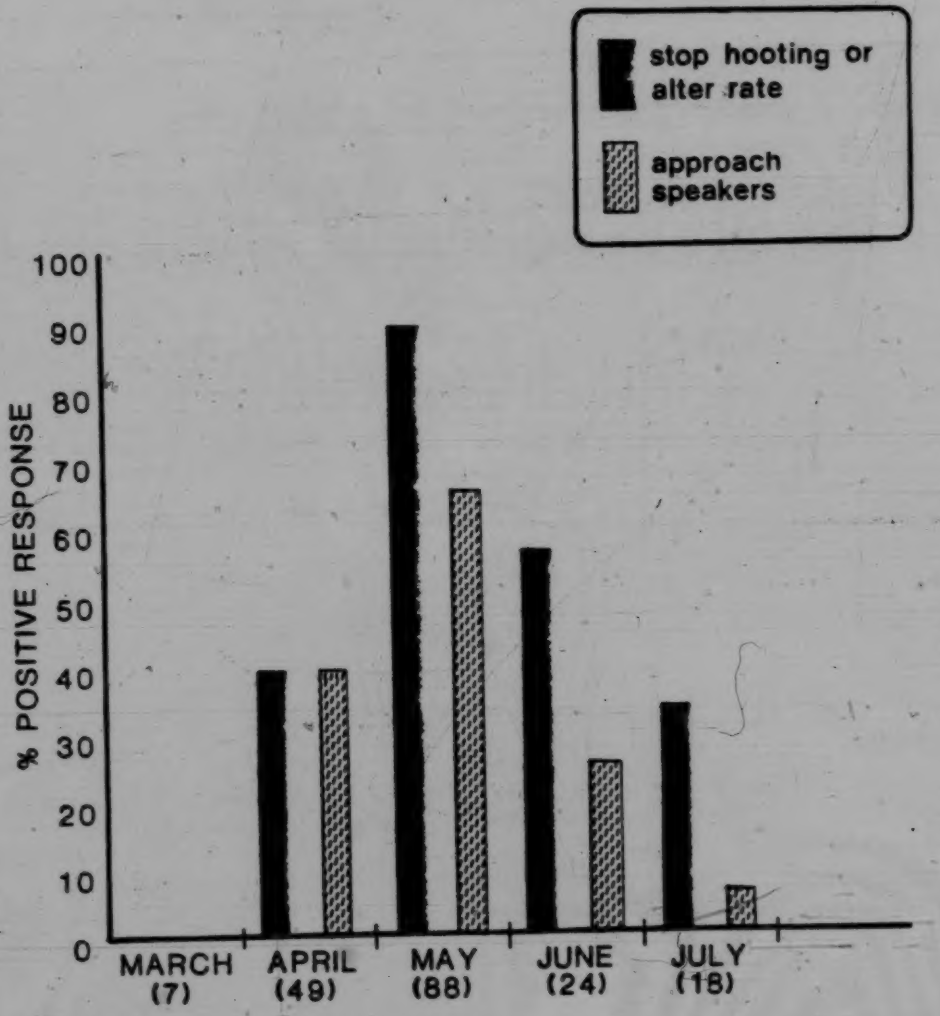

Figure 2 Response of Male Blue Grouse to Playbacks of Whinnies (sample size in parentheses)

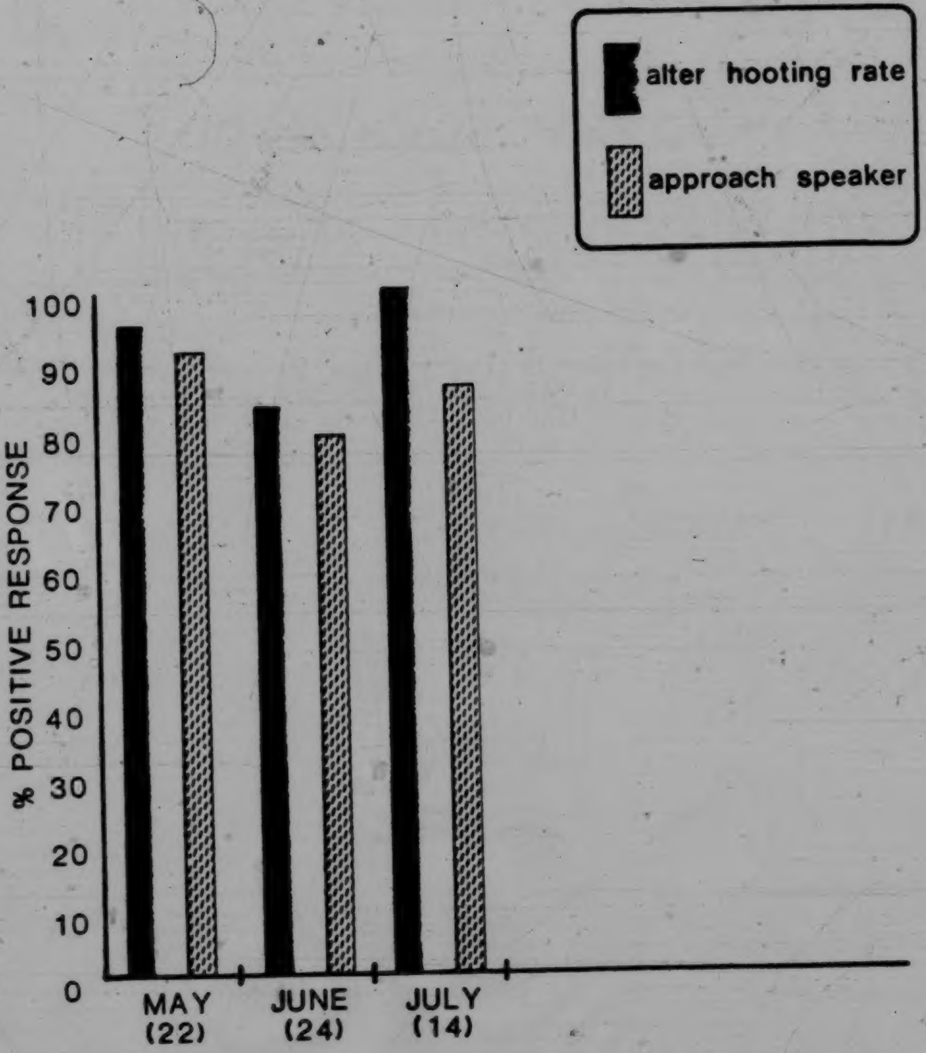

Figure 3 Responses of Male Blue Grouse to Playbacks of Brood Clucks (Sample in parentheses)

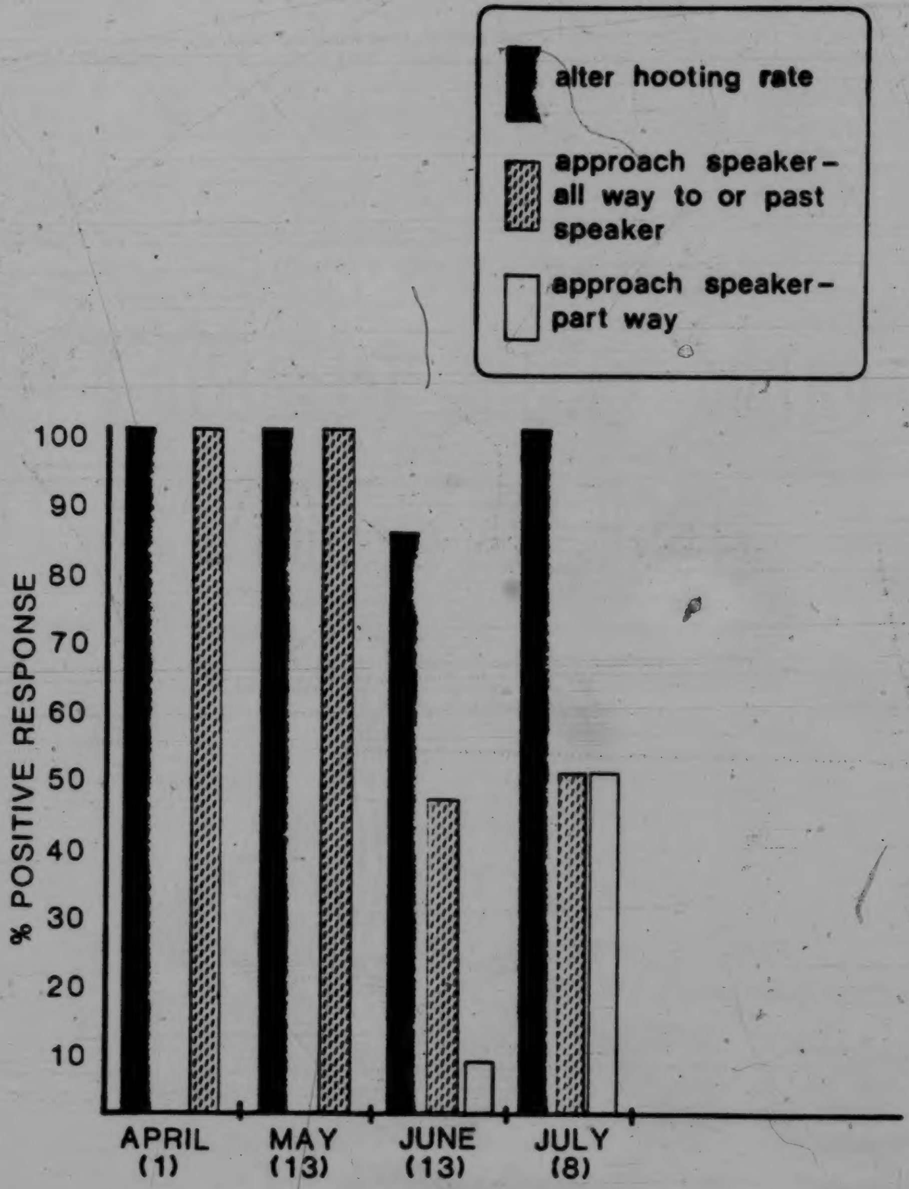

Figure 4 Responses of Male Blue Grouse to Playbacks of Liquid Clucks (sample size in parentheses)

LITERATURE CITED

ANDREW, R.J. 1956. Some remarks on behaviour in conflict situations. Brit. J. Anim. Behav. 4: 41-45.

ANDREW, R.J. 1961. The displays given by passerines in courtship and reproductive fighting: a review. Ibis 103a: 315-348, 549-579.

ARMSTRONG, E.A. 1947. Bird display and behaviour: an introduction to the study of bird psychology. Second ed. Dover, New York.

ARMSTRONG, E.A. 1973. A study of bird song. Second ed. Dover, New York.

BENDELL, J.F., AND P.W. ELLIOTT. 1967. Behaviour and the regulation of numbers in Blue Grouse. Can. Wildlife Serv. Rept. Ser. No. 4.

BERGERUD, A.T., AND H.D. HEMUS. 1975. An experimental study of the behavior of Blue Grouse (Dendragapus obscurus). I. Differences between the founders from three populations. Can. J. Zool. 53: 1222-1237.

BLACKFORD, J.L. 1958. Territoriality and breeding behavior of a population of Blue Grouse in Montana. Condor 6:, 145-158.

BLACKFORD, J.L. 1963. Further observations on the breeding behavior of a Blue Grouse population in Montana. Condor 65: 485-513.

BOAG, D.A. 1966. Population attributes of Blue Grouse in southwestern Alberta. Can. J. Zool. 44: 799-814.

BROOKS, A.C. 1926. The display of Richardson's Grouse, with some notes on the species and subspecies of the genus Dendragapus. Auk 43: 281-287.

BROOKS, R.J., AND J.B. FALLS. 1975. Individual recognition by song in White-throated Sparrows. III. Song features used in individual recognition. Can. J. Zool. 53: 1749-1761.

COOPER, C.R. 1977. Differences in behaviour between populations of captive Blue Grouse. M.Sc. thesis, Univ. Toronto, Toronto.

DONALDSON, J.L. 1973. A behavioral and demographic study of an insular population of Blue Grouse. B.Sc. Thesis, Univ. Victoria, Victoria.

EMLEN, S.T., J.R. RISING, AND W.L. THOMPSON. 1975. A behavioral and morphological study of sympatry in the Indigo and Lazuli buntings of the Great Plains. Wilson Bull. 87: 145-179.

FALLS, J.B. 1969. Functions of territorial song in the White-throated Sparrow. pp. 207-232 in HINDE, R.A. (Editor). Bird vocalizations, their relation to current problems in biology and psychology. Cambridge Univ. Press, Cambridge.

FALLS, J.B., AND M.K. MC NICHOLL. in press. Neighbor-stranger discrimination by song in male Blue Grouse. Can. J. Zool.

HARJU, H. 1974. An analysis for some aspects of the ecology of Dusky Grouse. Ph.D. thesis, Univ. Wyoning, Laramie.

HEMUS, H.D. 1972. A behavioural and demographic comparison of three Blue Grouse populations released on Moresby Island, B.C. B.Sc. (HONS) thesis, Univ. Victoria, Victoria.

HINDE, R.A. 1964. Display. pp. 202-205 *in* THOMSON, A.L. A new dictionary of birds. McGraw-Hill, New York.

HJORTH, I. 1970. Reproductive behaviour in Tetraonidae with special reference to males. Viltrevy 7: 184-588.

HOFFMAN, R.S. 1956. Observations on a Sooty Grouse population at Sage Hen Creek, California. Condor 58: 321-337.

KREBS, J.R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. Ecology 52: 2-22.

KRISTENSEN, J. 1973. Studies on interactions among female Blue Grouse.

Progr. Rept., mimeo, Univ. Alberta, Edmonton.

LACK, D. 1940. Pair-formation in birds. Condor 42: 269-286.

LACK, D. 1974. Evolution illustrated by waterfowl. Blackwell Sci. Pub., Oxford.

LOW, D.J. 1974. Qualities of individuals in a replacement stock of Blue Grouse. M.Sc. Thesis, Univ. British Columbia, Vancouver.

LUMSDEN, H.G. 1970. The shoulder-spot display of grouse. Living Bird 9: 65-74.

MARTIN, K. 1973. Breeding density and reproductive success of Robins in relation to habitat structure on logged areas of Vancouver Island, British Columbia. M.Sc. thesis, Univ. Alberta, Edmonton.

MC NICHOLL, M.K. 1978a. Territories of male Blue Grouse on Vancouver Island. in Ph.D. thesis, Univ. Alberta, Edmonton.

MC NICHOLL, M.K. 1978b. Postures and displays of male Blue Grouse. in Ph.D. thesis, Univ. Alberta, Edmonton.

MC NICHOLL, M.K. 1978c. Vocal communication among male Blue Grouse. in Ph.D. thesis, Univ. Alberta, Edmonton.

MOSSOP, D.H. 1971. A relation between aggressive behaviour and population dynamics in Blue Grouse. M.Sc. thesis, Univ. British Columbia, Vancouver.

PETRINOVICH, L., AND H.V.S. PEEKE. 1973. Habituation to territorial song in the White-crowned Sparrow (Zonotrichia leucophrys). Behav. Biol. 8: 743-748.

SIMARD, B.R. 1964. The testicular cycle of Blue Grouse (Dendragapus obscurus fuliginosus) and its relation to age, breeding behaviour and migration. M.Sc. thesis, Univ. British Columbia, Vancouver.

STEIN, R.C. 1963. Isolating mechanisms between populations of Traill's

Flycatchers. Proc. Amer. Phil. Soc. 107: 21-50.

STETTENHEIM, P. 1972. The integument of birds. pp. 1-63 in FARNER, D.S., AND J.R. KING. (Editors). Avian biology. Vol. 2. Academic Press, New York.

STIRLING, I., AND J.F. BENDELL. 1966. Census of Blue Grouse with record calls of a female. J. Wildl. Manage. 31: 28-34.

STIRLING, I., AND J.F. BENDELL. 1970. The reproductive behaviour of Blue Grouse. Syesis 3: 161-171.

TINBERGEN, N. 1948. Social releasers and the experimental method required for their study. Wilson Bull. 60: 6-51.

VERNER, J., AND M.M. MILLIGAN. 1971. Responses of male White-crowned Sparrows to playback of recorded song. Condor 73: 56-64.

ZWICKEL, F.C. 1972. Removal and repopulation of Blue Grouse in an increasing population. J. Wildl. Manage. 36: 1141-1152.

ZWICKEL, F.C., AND J.F. BENDELL. 1972. Blue Grouse, habitat and populations. Proc. Internatl. Ornithol. Congr. 15: 150-169.

PAPER 3. VOCAL COMMUNICATION AMONG MALE BLUE GROUSE

From 1971 to 1974 I studied social behavior among male Blue Grouse (Dendragapus obscurus) on Vancouver Island, British Columbia. Communication is an important component of social behavior, and thus the study of social systems. Blue Grouse spend a major portion of their time hooting, a sound generally considered to constitute song (Blackford 1963; Bendell and Elliott 1967; Stirling and Bendell 1970; Hjorth 1970). It appears to function in both courtship and territorial activities (McNicholl 1978a) and to be an important signal of grouse when visually isolated from each other (Stirling and Bendell 1970). Thus, hooting fits the usually accepted concept of song (Smith 1963; Thorpe 1964; Falls 1969; Lein 1972; Armstrong 1973). Since hooting thus appears to be a major communication vehicle in this species, I studied the use of this sound among male Blue Grouse in some detail.

STUDY AREA AND METHODS

The principal study area was a portion of Comox Burn (Zwickel 1972), situated approximately 19 km northwest of Courtenay, British Columbia. Further details on the general area are given by Zwickel (1972) and Martin (1973), and on the specific territories of the principal subjects of my study by McNicholl (1978c).

Detailed observations and experiments were conducted on approximately 20 males each year (36 principal subjects), most of which were color-banded (33 of 36), and individually identifiable. Data on song were normally gathered out of sight of the bird and its identification confirmed after the observational period. Routine data were collected for a minimum of 10 min prior to any experiments, at times of day ranging from dawn to dusk. These included number of syllables per song, time per song, interval of time between songs, and which neighbors were and were not singing. Similar data were collected during and for 10 min after experiments, when feasible.

I assessed seasonal trends in hooting by three methods. In 1972, I obtained a gross index by evening counts conducted at one site at a standard time. As a second index, I developed a scale of hooting for use by census crews. Thirdly, each time I visited a territory, I noted the hooting activity of the resident male and his neighbors. Visits to territories were planned for experimental purposes and other hooting records were obtained incidentally whenever I was on or near a male's territory. If no data on hooting activity on a male with which I worked regularly had been gathered for three days, I visited his territory to obtain such data.

I conducted hooting counts in 1972 on a regular basis at a constant location selected for good audibility. Prior to running these counts, I checked my reliability in hearing singing birds by conducting counts at four different localities in company with, but independently of, four other observers. These counts showed little variability among observers (McNicholl 1973). My counts were conducted each evening from 22 May to 25 May inclusive, and on every second evening thereafter to late August, except for 3 to 14 July and 10 to 20 August, and on four other dates missed due to weather or other factors. Each count was run from 20:45 to 21:45, and consisted of six 3-minute intervals (minutes 0-3, 10-13, 20-23, 35-38, 45-48, and 55-58) during which all hoots, whoots (Stirling and Bendell 1966) and number of male Blue Grouse singing were recorded.

Other details of behavior, weather, and other factors were noted in intervals between these counting periods. As this method was time consuming, and as the trends were similar to those shown by the two other methods, they were discontinued after 1972.

In 1972 I compared results of the hooting counts with the proportion of males hooting of all those encountered by census crews, and to hooting ratings collected by G.J. Goth, F.C. Zwickel and me. Since these two methods showed parallel trends to those obtained through hooting counts, I asked all observers to rate hooting at standardized times in 1973 and 1974. Ratings were conducted on even hours in a scale of 0 to 5. The numbers 0 to 4 referred to numbers of birds heard hooting, whereas 5 referred to 5 or more birds.

Singing of individual birds was also used to examine seasonal trends and to document daily trends and individual variation in hooting behavior.

In 1971, I noticed that I was rarely near a hooting bird without hearing at least one other grouse singing. In 1972, I collected data on this point systematically, supplementing these data with hooting count observations. In 1973 and 1974, I continued these observations and conducted experiments involving the stopping of one bird within a hooting group, to see whether his cessation would influence the hooting of neighbors. In addition, when birds were stimulated to hoot or to change hooting rate in response to playbacks of male or female grouse calls (McNicholl 1978a), I noted whether neighbors responded. One indication from these experiments was that the hooting of some birds dominated that of others. This led me to check patterns in initiation of singing in the early morning.

RESULTS

Description of hooting. - Hooting, referred to as a "booming call" (Skinner 1927; Grinnell and Storer *fide* Bent 1932), "drumming" (Blackford 1958), and "grunting" (Dawson *fide* Bent 1932; Blackford 1963), consists of a series of notes of low frequency (Edson 1925; Brooks 1926; Bent 1932; Blackford 1963; pers. obs.). Hjorth (1970) found frequencies of *D. o. fulinginosus*, the race on Vancouver Island, to range from 110 to 150 Hz, higher than for other races.

Male Blue Grouse vary the loudness of the song, thus enabling themselves to be heard at varying distances, a phenomenon I frequently noted and also mentioned by Hjorth (1970) and Stirling and Bendell (1970).

The apparent ventriloqual effect of this song, noted by several authors (Edson 1925; Brooks 1926; Johnson 1929; Haskins *in* Bent 1932; Grinnell and Storer *fide* Bent 1932) varied with its loudness and location of the bird in relation to the observer. Like Brooks (1926), I usually found the direction to be determined easily at a distance, such as on an adjacent territory, but the precise direction when close to the bird was sometimes difficult to discern if the bird was hooting softly. A common response by a hooting bird on my appearing close by was to soften the song, causing the sound to appear to come from a location 1 to 3 m from the original spot, even though I could usually see that the bird had not moved (McNicholl 1978b).

On Comox Burn, routine hooting consisted of songs of five to seven syllables, with six most common. Full songs rarely deviated from 3.0 secs in duration.

Hjorth (1970) and Stirling and Bendell (1970) show graphic illustrations of hooting. Johnson (1929) drew attention to the two note nature of the first and fifth syllables, and descriptions of hooting by Edson (1925), Brooks (1926), and Bent (1932) show that these authors were aware of at least some difference among syllables. The first syllable sounds double because of the intake of air on commencement (Blackford 1963) and the fifth is a distinct double note (see Hjorth 1970; fig. 43). I found this double note to occur on the fifth syllable of all six- and seven-syllable songs, and on most five syllable songs. This was confirmed by examination of sonograms in the laboratory of J.B. Falls.

On Comox Burn male Blue Grouse usually sang one to four syllables on beginning to hoot late in the season, but usually started with at least five syllables during the peak breeding season (Table 1). When approaching playbacks of female grouse calls, males almost invariably reduced the number of syllables in the song. On approaching playbacks of hooting, they reduced the number of syllables per song much less frequently.

Brooks (1926) and other early authors noted that D. o. fuliginosus "always(?)" hooted from high up in trees. I did not observe D. o. fuliginosus hooting in trees on Comox Burn, where tall trees were scarce, but saw males singing on the ground, on top of stumps, on crests of hills, and under trees. Hooting in trees has since become more common there, as the trees have grown higher (F.C. Zwickel pers. comm.). Hooting in conspicuous places and at elevated heights occurred shortly after females arrived.

Soft hooting. - Male Blue Grouse frequently lowered the volume of hooting in the presence of an observer, as noted by Blackford (1963) and

Stirling and Bendell (1970). Hooting became softer when female calls were first played, then increased to the previous volume shortly thereafter, unless the bird stopped singing altogether. Intruding males also used soft hoots in the presence of a live or dummy hen, but only if the resident did not appear (McNicholl 1978a). Stirling and Bendell (1970) stated that males also give softer hoots when hooting alone.

Seasonal trends in hooting. - Results of my evening hooting counts of 1972 are summarized in Table 2. These data show a higher rate of hooting in late May and June than later in the year. In fact, later averages were inflated by occasional evenings in which bursts of hooting occurred throughout the hour or part of it in weeks during which little or no hooting occurred on other evenings. Thus, in May, the rate of singing was high on all nights, whereas hoots per hour ranged widely in June and later (Table 2).

Hooting ratings for 1973 and 1974 are summarized by two week periods in Fig. 1, from 1 April to 20 August. These data show very little singing activity prior to late April in either 1973 or 1974. In addition, records from 16-31 March 1974 all consisted of "0"; in fact observers usually noted "no hooting all day" on their daily field cards during this period. Males arrived on the study area, starting in mid-March. Hooting increased in late April and early May (Fig. 1), followed by a general decrease in late May, June, July and August, but with occasional bouts of hooting into August. Nine additional ratings from 21-27 August 1973 were all "0."

My notes on hooting activity of individual birds showed the same general seasonal trends noted by the other two methods, with some variation in timing among years (Table 3).

Daily Hooting Patterns. - Data on daily hooting patterns were obtained from general notes, hooting counts, and early morning observations conducted to determine which individuals in specific groups initiated singing. Data summarized in Fig. 2 show that during the peak breeding season (May), hooting peaks in early morning and late evening, as noted by others (Edson 1925; Bendell 1955; Fowle 1960; Hjorth 1970; Stirling and Bendell 1970). This pattern is less evident later in the season, although Table 4 shows that after May, an increase in hooting occurred during the last hour before dark, with more hooting by the end of the hour than early in the hour.

During the peak breeding season, a high level of hooting was usually maintained all day (Fig. 2), as reported by Stewart (1967). Later in the season, all day singing was less common, but was more frequent on cloudy days than on sunny days as illustrated by a higher proportion of birds encountered singing under cloudy conditions (Table 5). In the early morning, hooting started later on cloudy mornings than on clear days (Table 6). Commencement of hooting of all birds was not determined by precise light conditions, as different groups under essentially identical light conditions began singing as much as 30 to 40 min apart on the same morning (Table 6).

Individual hooting patterns. - The tendency of individual males to sing can be measured crudely as the proportion of records during April to June in which the bird was hooting. In Table 7, such hooting persistence is indicated for 34 individuals, arranged by greatest tendency to sing. Considerable variation in hooting tendency is evident among individuals.

Extensive records were kept of hooting patterns of individual birds, with number of syllables per song, duration of song, and time intervals between songs noted. These records are summarized in Table 8. As noted by Stirling and Bendell (1970) very little variation occurred in duration of song; in fact only 8 of 42 birds showed any deviation from 3.0 sec per song, and these deviations were so rare as to appear in mean values for these birds only at two (2 cases) to three (6 cases) decimal places. Number of syllables per song varied more. Ten birds showed no deviation from 6 syllable songs, and 23 birds deviated from 6 syllables only rarely, occasionally singing 5 or 7-syllable songs. Three rarely deviated from 5 syllable songs, and one routinely sang 7-syllable songs or interspersed these with 6-syllable songs.

Intervals between songs reported in Table 8 are highly variable both within and between individuals. Prolonged intervals were more frequent early and late in the season, and individuals varied according to time of day, activity of other birds, and prior disturbance. However, some birds routinely hooted at a faster rate than others.

Song in relation to hooting by other males. - In 1972 my data on 123 cases of hooting on Comox Burn showed that other birds were also hooting in 118 cases, with only five instances in which I could not hear another bird. In four of the five exceptions, there were long intervals between the songs of one bird; in fact one bird sang only two songs in 10 minutes. In another case, the bird stopped hooting before the end of the 10 min observation period in which I was noting intervals between songs. During the 1972 hooting counts, I found that the initiation of hooting by one bird was rapidly followed by the commencement of another from the same direction, and similarly the cessation of singing by one was followed rapidly by the cessation of singing by another. These observations and similar comments by others (Blackford 1958; Bendell and Elliott 1967) led me to believe that one bird might influence the singing of another.

Observational data in 1973 and 1974 again showed the rarity of birds hooting alone, and the usual commencement of another or cessation of the first in the few cases of lone hooting that were observed (Table 9).

Table 10 shows the results of experiments conducted in 1973 and 1974 to test the influence of hooting by one bird on the singing of others. These results show that if two birds were hooting together (alternating), stopping one usually stopped the other. In the eight cases where this did not occur, the second bird began to alternate with other birds, or a previously silent bird began to hoot with the remaining bird. If three birds were alternating, stopping one had one of two effects: both others stopped hooting, or the slower of the remaining two changed his rate to match that of the faster bird.

Similarly, the stimulation of a bird to sing by playing back other grouse calls (hooting or female calls) caused the neighbor to start singing shortly after the subject began, and causing one bird to alter its rate of song caused the neighbor(s) with which he was singing to alter their rates.

Thus, both observations and experiments provide strong evidence that singing of individual males is influenced by that of their neighbors.

Hooting dominance. - In the three-bird hooting groups mentioned above, the three birds did not hoot with equal frequency, but rather one bird (A) hooted twice as often as either of the others (B and C) in a sequence: A, B, A, C, A, B, A, C, A, etc. If the bird which hooted most often (A) was stopped, both others stopped, but if either of the others (B or C) was stopped, the remaining bird of B and C began to sing more frequently to match the rate of A. In addition if A was hooting with only one partner, stopping A resulted in rapid cessation of singing by his partner, whereas the stopping of the partner caused A to stop only after 8 to 15 minutes (Table 11). Within particular hooting groups, A birds were consistently the same individuals, but some birds were A in one group and B or C in another. A birds were not necessarily the oldest birds, and the few data available on status of "replacement" birds in territories vacated by A birds indicate that dominant status is not automatically associated with particular territories (Table 11).

In early morning, singing was initiated within groups by "A" birds of the above experiments. The hooting of a particular A bird was followed almost immediately by that of one or more of his regular hooting partners (Table 6). On any given morning, different groups began singing at distinctly different times, emphasizing this association.

These data indicate that certain birds were "dominant" over others in hooting. One such male even dominated another in the latter's territory on one occasion; the latter left when the former approached a female dummy plus female call.

DISCUSSION

Description of hooting. - The low frequency in sound of hooting by Blue Grouse was referred to by Dawson (*fide* Bent 1932) as among the lowest in nature, and Greenwalt (1968) listed only the Spruce Grouse (*Canachites canadensis*) as having a song of lower frequency.

The marked difference in distance noted by Brooks (1926) and

Blackford (1958) at which hooting could be heard is likely exaggerated, as Skinner (1927) reported that the song of _D. o. richardsoni_, one of the races alleged to be harder to hear, could be heard at great distances, and _D. o. fuliginosus_ vary the loudness of song frequently.

The apparent ventriloqual effect produced by lowering the volume of singing may be either true ventriloquism, or an artifact of surroundings, with the sound being deflected by rocks or trees. Lowering the sound in the presence of the female may be of advantage in allowing the female to hear the male, but reducing the chances of predators detecting the increase in activity caused by the presence of the female. In addition, Knight (1974) has noted that birds are able to determine directionality of sound more accurately than mammals. Thus, the apparent ventriloqual effect produced by lowering the volume of song may not confuse the female grouse, but could confuse a mammalian predator long enough to allow the grouse to escape more readily. In addition, quiet songs may convey a reduced attack tendency (see below).

Brooks' (1926) description of the song suggests a double note on the fourth syllable in a five-syllable song, and another description by Grinnell and Storer (_fide_ Bent 1932) suggests that both the fourth and fifth syllable differed from the first three. Edson (1925), Bent (1932), and Johnson (1929) all place the double note on the fifth syllable, thus agreeing with my data. These reported differences may be due to race.

Edson (1925) noted that the last (fifth) and even fourth syllables were sometimes omitted from songs of Blue Grouse. This may also be an attribute of race, but I suspect the grouse he heard omitted these syllables in response to his presence or had just begun singing. The fact that number of syllables per song was reduced on approaching female calls but rarely when approaching male calls suggests that fewer syllables than usual may convey lack of aggressive intent. The greater tendency to sing shorter songs late in the season, when motivation to defend territories may be reduced, is consistent with this interpretation. On the other hand, reducing number of syllables on approach may be an artifact of increased "emotional" excitement. The bird may stop to sing, but commence moving again before completing the song. This interpretation suggests that the presence of a female on territory may cause a stronger response than the presence of an intruding male, at least initially, but also is more consistent with the occasional dropping of a syllable in response to a male. Some "intrusions" by other males may seem more threatening than others because of precise location, previous intrusion, or other factors.

The greater tendency to sing at elevated sites shortly after the arrival of females is probably a strong proclamation of the residence of a territorial male. At this time, yearlings and possibly non-territorial adults arrive in addition to females. Males do not approach playbacks of hooting on their territories aggressively until this period, but at this time approach such playbacks, presumably to defend their territories (McNicholl 1978a). Thus, hooting from higher elevations may serve the dual functions of "advertising" the location of the male to hens and also repelling would-be intruders.

Soft hooting. - Soft hooting appears to be merely a quiet version of hooting, and not of a different duration, and thus does not fit Thorpe's (1961, 1964) complicated criteria of sub-song. Thus soft hooting would be better considered as "quiet song" or as a type of "secondary song," in the sense used by Lister (1953), i.e. songs with lower volume than normal.

My results partially contradict the statement by Stirling and Bendell (1970) that hooting becomes louder when recording of the "whinny" (a female call) is played. Rather, I found that hooting became softer when female calls were first played, then increased to the previous volume. The fact that adult male Blue Grouse lower the volume of their hooting on approaching a female is consistent with the view that quiet songs may convey a reduced attack tendency (e.g. Ficken 1962; Dunham 1966; Morse 1966, 1967; Kroodsma 1974; Brooks and Falls 1975), though this does not necessarily imply a greater escape tendency (Kroodsma 1974). Intruding males, thought to be yearlings or young, non-territorial adults also hoot softly near females if the resident male is slow to appear (McNicholl 1978a). Their soft hooting may also convey low attack tendency to the female, but would also reduce the chance of their being detected by the territory holder. Such males sing at full volume on the rare occasions when they aquire a territory. The few instances in which I found Blue Grouse singing alone were late in the season, when territorial defence is presumably weak. Thus, the report by Stirling and Bendell (1970) that males give softer hoots when singing alone is also consistent with the interpretation of lower attack tendency.

Seasonal trends in hooting. - The seasonal pattern of hooting reported in this study is consistent with that known for other populations of Blue Grouse (Bendell 1955; Hoffman 1956; Fowle 1960; Blackford 1963; Stirling and Bendell 1966; Bendell and Elliott 1967; Stewart 1967; Low 1974), and for birds in north temperate regions in general (Thorpe

1961; Armstrong 1973 and many others). The initial period of silence after the return from the wintering areas to their territories has been noted by Blackford (1963) and Bendell and Elliott (1967), and caused Harju (1974) to suggest that hooting did not have a territorial function. However, experiments with playbacks of grouse calls showed that males hoot in response to any intruding grouse (McNicholl 1978a); suggesting that hooting functions as both courtship and territorial song, a duality shared with most bird species that sing (Lein 1972). Furthermore, when playbacks of hooting are accompanied by dummies of both sexes, males will interact with (i.e. attack) the male dummy rather than the female dummy (McNicholl 1978a), suggesting that a hooting male on the territory is considered by the bird as a distinct threat. The onset of hooting coincides generally with the time of arrival of hens and yearling males (Zwickel and Bendell 1967; Bendell and Elliott 1967). This suggests that females stimulate seasonal initiation of hooting, especially as yearlings are tolerated hooting within the territory for a brief period (McNicholl 1978a). However, such intruders are expelled if seen, and are also soon approached and expelled (or attacked) if heard hooting, again suggesting that hooting serves both courtship and territorial functions. Territorial males usually return to the same territory each year (McNicholl 1978c). Since most likely contestants for territories are likely to be yearlings, or possibly two-year old males, birds hooting within a territory early in the season are more likely to be migrants en route to their own territory, and thus little threat. Thus, the low level of hooting early in the season and lack of aggressive approach to playback of hooting then does not mean that hooting is not a territorial song in addition to its courtship function. The most active period of hooting is the most active period of both mating and potential territory loss, but active hooting extends well beyond nest initiation by hens (see Zwickel 1977). Occasional singing bouts in late July and August seem more likely proclamations of territory than courtship songs.

Daily Hooting patterns. - The daily pattern of morning and late evening peaks in hooting is also consistent with reports of others (Edson 1925; Bendell 1955; Fowle 1960; Hjorth 1970). Wing (1946) and Harju (1974) noted similar patterns in "drumming flights" of interior races. Early morning and late evening peaks are common in bird song (Thorpe 1961; Armstrong 1973).

The daily pattern observed is consistent with a pattern of activity in general. Light is undoubtedly an important releaser of singing in early morning, as indicated by differences in singing times depending on cloud cover in early morning (see also Hjorth 1968). Active hooting early in the morning corresponds to activity by nesting hens, which leave nests then to feed (Bendell 1955). Initial singing, however, appears to occur before much activity by males, and is likely a direct response to the rising sun, although different males apparently respond to different levels of light, as not all singing groups started at the same time. Hooting throughout the day during the active nesting period also corresponds to the generally higher rate of activity by birds at that season, when males are courting females, and also actively defending territories. Both early morning and late evening peaks in singing may function primarily as a declaration of the presence of territorial males in their correct territories. As males are able to distinguish the songs of their neighbors from those of other male Blue Grouse (Falls and McNicholl in press), such a burst of singing would readily inform each bird of changes in the social organization of his surrounding area, and thus warn him of parts of his territory which may be contested by new birds.

Individual hooting patterns. - The variability in singing tendency among males has also been noted for other birds (Armstrong 1973). The lack of variation in duration of song indicates that this feature is of little value in distinguishing individuals or motivation of birds singing. Number of syllables per song may be of limited value in distinguishing individuals in some cases, such as the bird which usually sang seven-syllable songs, but as most birds regularly sang six-syllable songs, this feature probably has little value in individual recognition. As indicated above, however, number of syllables reflects motivation to some extent.

The five to seven syllable songs reported in this study are comparable to other records in the literature: five (Edson 1925), five to rarely six (Brooks 1926), five (Johnson 1929), four to six (Bent 1932), five to seven, average six (Blackford 1958), six or rarely seven (Stirling and Bendell 1970), and four to six, depending on race (Hjorth 1970).

Bent (1932) reported a series of 13 intervals between songs in one *D. o. fuliginosus* as 12 to 32 secs (mean 20.5). Bendell and Elliott (1967) reported six hoots per minute in time of high excitement, and Stirling and Bendell (1970) reported a range of 0 to 10 hoots per min in this race. At ten hoots per min, the interval would average 3.3 secs, assuming nine intervals and a duration of 3.0 sec per song. The intervals I report are far more variable than these and those reported for other races by Harju (1974), Rogers (fide Johnsgard 1973), Stewart (1967), and Grinnell and Storer (fide Bent 1932). My data are summarized from a relatively large number of individuals, and over the entire breeding season. This variability in intervals between songs undoubtedly reflects motivation or "emotional state" of the bird singing. Intervals tend to be shorter during the peak of the breeding season, probably reflecting increased courtship and territorial behavior. Individual variability is not strictly a function of dominance, because the singing of each bird influences the singing of its neighbors. Thus, dominant birds which sing frequently have neighbors which also sing frequently, whereas dominant birds which rarely sing have neighbors which seldom sing. Since intervals vary with season, time of day and activity of other birds (for both sexes), individual variability in tendency to sing is likely of little value in individual recognition.

Song in relation to hooting by other males. - The influence on hooting of an individual by the hooting of other birds corresponds to singing in passerines (Thorpe 1961, 1964; Armstrong 1973: and others). Wing (1946) and Harju (1974) have also suggested such a relationship between display flights in inland races of this species, and Aubin (1972) for the drums of the Ruffed Grouse (Bonasa umbellus). This communication among males may play a key role in the social organization of Blue Grouse, as suggested below.

Hooting dominance. - Dominance hierarchies are a common feature of lek social systems in grouse and other birds (Armstrong 1947, 1964; Brown 1964; Dorst 1971; Hartzler 1972; Wilson 1975), but are usually not considered to be a component of the social organization of territorial species (Wilson 1975.). My results, however, suggest that some male

Blue Grouse dominate others in singing, and that definite social groups participate in hooting. Whether or not such "dominant" males are truly dominant, with the "dominant" singer predictably dominant over the other(s) of his social group (Crook 1964), is unknown. However, the one case in which such a "dominant" singer dominated another bird on the latter's own territory does suggest that such singing dominance reflects true dominance.

The role of song in the social organization of Blue Grouse. - Several authors have reviewed the features and advantages of territorial and lek (or dominance) social systems, both in birds in general (e.g. Fisher 1954; Snow 1963; Armstrong 1964; Brown 1964, 1974; Crook 1965; Lack 1966; Alexander 1974; Wilson 1975) and in grouse (e.g. Wing 1946; Hamerstrom and Hamerstrom 1960; Hartzler 1972; Johnsgard 1973; Ballard and Robel 1974; Rippin and Boag 1974; Wiley 1974). Traditionally, territorial and hierarchical systems are regarded as separate types of social systems. For example, Wynne-Edwards (1965) regarded social hierarchy as equivalent to territoriality, with both admitting a "limited quota of individuals" to share resources. More recently, Wilson (1975) regarded territory and dominance as separate manifestations in a continuously graded series. However, the social system of male Blue Grouse appears to combine elements of both territory and dominance, with song playing a major role in maintaining the system.

Two characteristics common to lek species exhibited by male Blue Grouse are the definite hooting groups or associations apparent in the population I studied, and apparent hierarchy of males, at least in singing. In addition slow approach by males to playback of female calls in spite of quick response by changing singing patterns (McNicholl

1978a), suggests that males resident on territory tend to wait for females to approach. On the other hand, Blue Grouse do occupy solitary territories from which other males are excluded (Bendell and Elliott 1967; McNicholl 1978c), and their territories are not restricted to the small dancing posts commonly held as territories by lek species. Thus, although Hjorth (1970) characterized Blue Grouse as a polygamous species with solitary display, their vocal behavior is socially oriented and males do aggregate during singing. Unlike lek species, they do not usually congregate at a dancing ground or arena (with possible exceptions in inland races: Wing 1946; Blackford 1958, 1963; Harju 1974), the territories are not abandoned during parts of the day when the communal display does not take place, and groups of females do not congregate nearby. Thus some features of lek systems are present while others are absent.

One advantage suggested for lek behavior is that females may select males who are genetically most fit, with dominance being an indication of genetic superiority (Trivers 1972). In such a system the majority of matings are effected by a few males but even these must mate quickly or subordinates interfere (Trivers 1972). If females can detect dominance through singing, they could select "superior" males with which to mate in a territorial species with singing dominance. These birds could then mate without interference.

Song probably indicates a territorial male is present, thus keeping other males from challenging his possession of the territory. It also probably attracts females to mate. Song may also help to identify individuals, as suggested by the ability of male Blue Grouse to distinguish songs of neighbors from those of non-neighbors (Falls and McNicholl in press). Klopfer (1962) noted the importance of individual recognition in social systems involving dominance.

I suggest that the social system of male Blue Grouse involves territorial birds which sing in distinct social groups. Within these groups, a dominance is present. Females mate only with territorial males, and perhaps mainly with those which dominate others in singing. Yearling males and some younger adults are "surplus" birds which quickly fill in territories of birds which have died. Evidence for such a "surplus" is strong, as residents removed either through natural deaths or experimental removals are replaced (Bendell _et_ _al_. 1972; Zwickel 1972). Observations during playback experiments using female calls (McNicholl 1978a), and other incidental observations, suggest that these birds remain on or near territories of resident males. Such birds are usually silent, although they will sing softly if the resident male is slow to approach a playback of a female call. Thus, such birds are likely watching for a vacancy, and song may be important in informing them that one is not available.

SUMMARY

Hooting by male Blue Grouse appears to be true song in the sense generally used (e.g. Thorpe 1961, 1964; Armstrong 1973), functioning in both courship and territorial contexts. "Soft hooting" is a form of quiet song used under situations in which males are not likely to exhibit aggression. Hooting reaches a peak about the time hens and yearlings arrive on the study area, and diminishes towards the end of the nesting season, with occasional bursts of activity later. The tendency for peak activity in bird song and other behavior to occur in early morning and late evening is manifest in hooting of Blue Grouse. On Comox Burn, most birds sing most often in 6 syllable songs of 3 sec duration, but individuals vary in syllables per song, and especially in frequency of singing. Male Blue Grouse tend to sing in groups of two or three in which the singing of some birds apparently dominates that of others. Song plays a key role in the social system of Blue Grouse, which combines elements of the lek system with those of more typical territorial systems.

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TABLE 1

PERCENTAGE OF INITIAL SONGS COMPOSED OF ONE TO SEVEN SYLLABLES SUNG BY MALE BLUE GROUSE DURING EACH MONTH ON COMOX BURN

Number of syllables	% occurrence in month (sample size)				
	April(126)	May (264)	June(150)	July(56)	August(15)
1	0	0	0.7	8.9	40.0
2	0	0.4	2.7	7.1	40.0
3	0	0.4	3.3	7.1	20.0
4	0.8	0.4	4.0	5.4	0
5	10.3	12.0	14.7	14.3	0
6	84.9	81.0	64.7	50.0	0
7	4.0	6.4	10.0	7.1	0

TABLE 2

WEEKLY TRENDS IN HOOTING FROM EVENING HOOTING COUNTS, 1972

Dates	Total Hoots/hour Mean'	Total Hoots/hour Range	Number males hooting/period
22-31 May	310	173-349	2-7
1-7 June	93	1-148	0-5
8-14 June	105	16-218	0-6
15-21 June	91	4-197	0-6
22-30 June	136	0-198	0-5
2 July	103	103	2
14-21 July	5	0-9	0-1
22-31 July	46	0-82	0-3
1-7 August	70	54-80	0-4
9 August	0	0	0
21-31 August	0	0	0

' Hoots totaled for each night (hour), and means of these totals determined.

TABLE 3

PERCENTAGE OF ENCOUNTERS WITH MALE BLUE GROUSE IN WHICH BIRD WAS HOOTING, 1972-1973 (SAMPLE SIZES IN PARENTHESES)

Dates	1972	1973	1974
16-31 March	----	----	0(24)
1-14 April	----	33(46)	6(50)
15-21 April	----	39(41)	17(63)
22-28 April	100(2)	76(98)	56(65)
29 April-5 May	77(73)	69(89)	77(64)
6-12 May	93(54)	65(83)	78(63)
13-20 May	99(95)	51(95)	70(83)
21-27 May	83(107)	28(122)	63(70)
28 May-3 June	64(42)	30(104)	51(81)
4-11 June	20(92)	21(100)	46(70)
12-18 June	17(90)	26(72)	15(34)
19-25 June	28(89)	20(101)	27(44)
26 June-2 July	25(89)	34(44)	37(43)
3-9 July	6(17)	24(37)	39(28)
10-16 July	2(42)	0(31)	33(12)
17-23 July	21(33)	20(15)	19(21)
24-30 July	3(35)	20(10)	12(83)
31 July-6 August	0(11)	0(9)	30(23)
7-13 August	0(16)	0(11)	13(24)
14-20 August	----	----	0(6)
21-27 August	0(5)	----	----
28-31 August	0(16)	----	----

TABLE 4

HOOTING ACTIVITY BY THREE-MINUTE PERIOD DURING HOOTING COUNTS, 1972

Period (Min. after start of count)	MEAN HOOTS/PERIOD				BIRDS HOOTING/PERIOD (MEAN)			
	May	June	July	August	May	June	July	August
0-3	48	16	6	6	5.0	2.0	1.0	1.0
10-13	45	17	5	6	5.3	2.4	0.8	0.8
20-23	47	15	10	8	4.3	2.2	0.8	0.8
35-37	51	17	9	8	4.2	2.8	1.0	1.5
45-47	48	20	8	8	4.7	2.8	1.0	1.3
55-57	50	24	8	12	4.4	2.9	1.2	1.3

TABLE 5

NUMBER OF MALES HOOTING COMPARED TO THOSE NOT HOOTING ON ENCOUNTERS ON COMOX BURN, JUNE-AUGUST, IN RELATION TO CLOUD COVER (SCALE OF 0-10)

Cloud Cover ':	0	1	2	3	4	5	6	7	8	9	10
No. Hooting	6	5	2	12	11	4	9	20	11	9	44
No. Not Hooting	22	16	14	16	3	2	2	4	1	3	4

' Scale of 0-10, where 0 = no visible clouds, 3 = 30% of sky covered by clouds, 10 = 100% cloud cover, etc.

TABLE 6

COMMENCEMENT OF HOOTING IN EARLY MORNING, COMOX BURN 1974

Date	Cloud Cover'	Time First Blue Grouse(A1) Sings*	Time(s) Other A Birds Sing*	Time Hooting Partner(s) Sing*
May:				
23	10	04:31	A(2): 04:42 A(3): 04:48	B(1): 04:32; B(2): 04:42; B,C(3): 04:48
24	10	04:40	A(2): 04:42 A(3): 04:54	B(1): 04:40; B(2): 04:42; B,C(3): 04:55
28	2	04:12	A(2): 04:24 A(3): 04:31	B(1): 04:13; B(2): 04:24; B(3): 04:31
29	4	04:16	A(2): 04:18 A(3): 04:24	B(1): 04:16; B(2): 04:18; B(3): 04:24
31	2	04:17	A(2): 04:23	B(1): 04:17; B(2): 04:32
June:				
4	3	03:57	A(2): 04:04 A(3): 04:12 A(4): 04:15 A(5): 04:18	B(1): 03:57; B(2): 04:04; B(3): 04:14; B(4): 04:15; B(5): 04:18
6	2	04:07	A(2): 04:08 A(3): 04:28	B(1): 04:07; B(2): 04:08; B(3): 04:18
7	2	04:06	A(2): 04:10 A(3): 04:28	B(1): 04:06; B(2): 04:10; B(3): 04:28
12	1	04:10	A(2): 04:11 A(3): 04:39	B(1): 04:11; B(2): 04:11; B(3): 04:39
20	2	04:01	A(2): 04:12	B(1): 04:01; B,C(2): 04:13

' Cloud Cover 0-10, as in Table 5.

* A birds dominate partners in singing. Groups for each morning are identified by numbers in parenthesis, with A the dominant, and B and C his singing partners, i.e. A(1) alternates with B(1) or B(1) and C(1).

TABLE 7

PERCENTAGE OF ENCOUNTERS IN WHICH INDIVIDUAL MALES WERE FOUND HOOTING. SAMPLE SIZES IN PARENTHESES

Bird	% Encounters Bird Hooting (Sample size)
1	72(60)
2	66(103)
3	65(92)
4	64(22)
5	62(134)
6	58(225)
7	58(26)
8	55(22)
9	54(46)
10	54(76)
11	52(27)
12	50(12)
13	50(149)
14	49(162)
15	48(60)
16	48(21)
17	47(98)
18	47(15)
19	46(102)
20	46(89)
21	46(103)
22	44(63)
23	43(84)
24	42(74)
25	40(43)
26	40(5)
27	40(15)
28	39(26)
29	38(58)
30	33(119)
31	29(14)
32	28(39)
33	27(88)
34	16(19)

TABLE 8

SUMMARY OF PARAMETERS OF HOOTING SHOWN BY 42 MALE BLUE GROUSE

Duration of song:

No. of birds with no deviation from 3 secs: 35

No. of birds deviating from 3 sec songs: 8

Range of duration: 2-4 secs, 1 bird; 3-4 secs, 7 birds

Sample sizes per bird: 39-998 (mean = 276)

Number of syllables per song:

No. of birds with no deviation from 6 sylls per song: 10

No. of birds with range of sylls/song of 4-6: 2

No. of birds with range of sylls/song of 4-7: 2

No. of birds with range of sylls/song of 5-6: 18

No. of birds with range of sylls/songs of 5-7: 8

No. of birds with range of sylls/song of 6-7: 2

Sample size per bird: 38-998 (mean = 277)

Range of intervals between songs (secs): 1-500

Range in mean interval per bird: 10.2-45.5 secs

Least range of intervals in one individual: 22 secs (3-25), mean 11.8 secs

Greatest range of intervals in one individual: 495 secs (5-500), mean 45.5 secs

Mean range of intervals within one individual: 116 secs (42 birds)

Sample size per bird: 37-975 (mean = 263)

TABLE 9

OBSERVATIONS OF HOOTING ASSOCIATIONS IN 1973 AND 1974

Association observed		Number of cases	% of cases
2 or more males are hooting		773	94.6
1 male hoots alone		44	5.4
- second male begins within 5 minutes	20		
- second male begins in 5-10 minutes	10		
- second male does not begin within 15 minutes; subject continues alone	6		
- subject stops within 5 minutes	8		
Total		817	100.0

TABLE 10

1973 AND 1974 EXPERIMENTS TESTING THE INFLUENCE OF ONE MALE'S HOOTING ON THAT OF OTHERS

Association	No.	%
2 males hooting together:		
- stopping one male stops other	146	94.0
- stopping one male does not stop other	8	5.2
3 males hooting together:		
- stopping one male stops both others	29	60.4
- stopping one male does not stop both others	19	39.6
4 males hooting together:		
- stopping one male stops other three	2	100.0
- stopping one male does not stop others	0	0.0
Causing one male to start hooting causes neighbor(s) to start hooting	4	5.8
Altering rate of one male causes neighbor(s) to alter rate	131	100.0
Altering rate of one male causes no neighbor to change rate	0	0.0

TABLE 11

OBSERVATIONS ON DOMINANCE IN HOOTING ASSOCIATIONS, 1974

Experiments on stopping hooting by male Blue Grouse:	
- stop A* bird:	
- singing partner(s) stop singing immediately:	104
- partner(s) continue singing:	0
- stop B* in associations of two birds singing:	
- A stops singing in less than 8 mins:	0
- A stops singing in 8-10 mins:	37
- A joins another singing group, whose birds alter rate accordingly:	7
- stop B or C* bird, when three birds hooting:	
- remaining bird of B or C speeds up hooting rate to match that of A:	21
- both A and the remaining of B or C stop:	0

Relative dominance of individuals:

Number of males always A birds: 7 (ages: 4-8+ years in 1974)

Number of males A in some groups, B in others: 11 (ages: 2-10+ years in 1974)

Number of males always B birds: 8 (ages: 2-7+ in 1974)

Replacement of males:

A replaced by A: 0; by A-B: 1; by B: 3.

A-B replaced by A: 0; by A-B: 1; by B: 0.

B replaced by A: 1; by A-B: 1; by B: 1.

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* A dominant bird in hooting associations; B and C "subordinates".

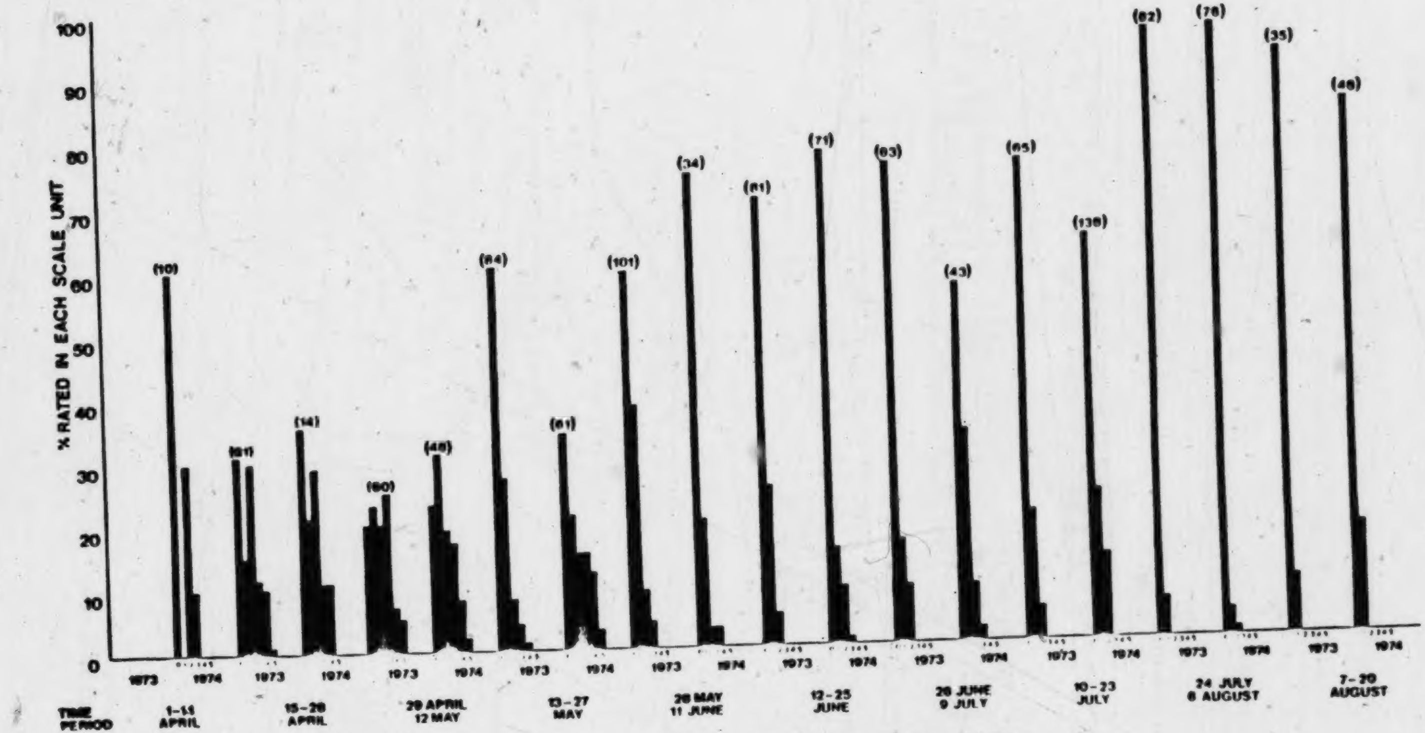

Figure 1 Summary of Hoot Ratings collected by various observers on Comox Burn in 1973 and 1974. Scale 0–5; Sample sizes in parentheses

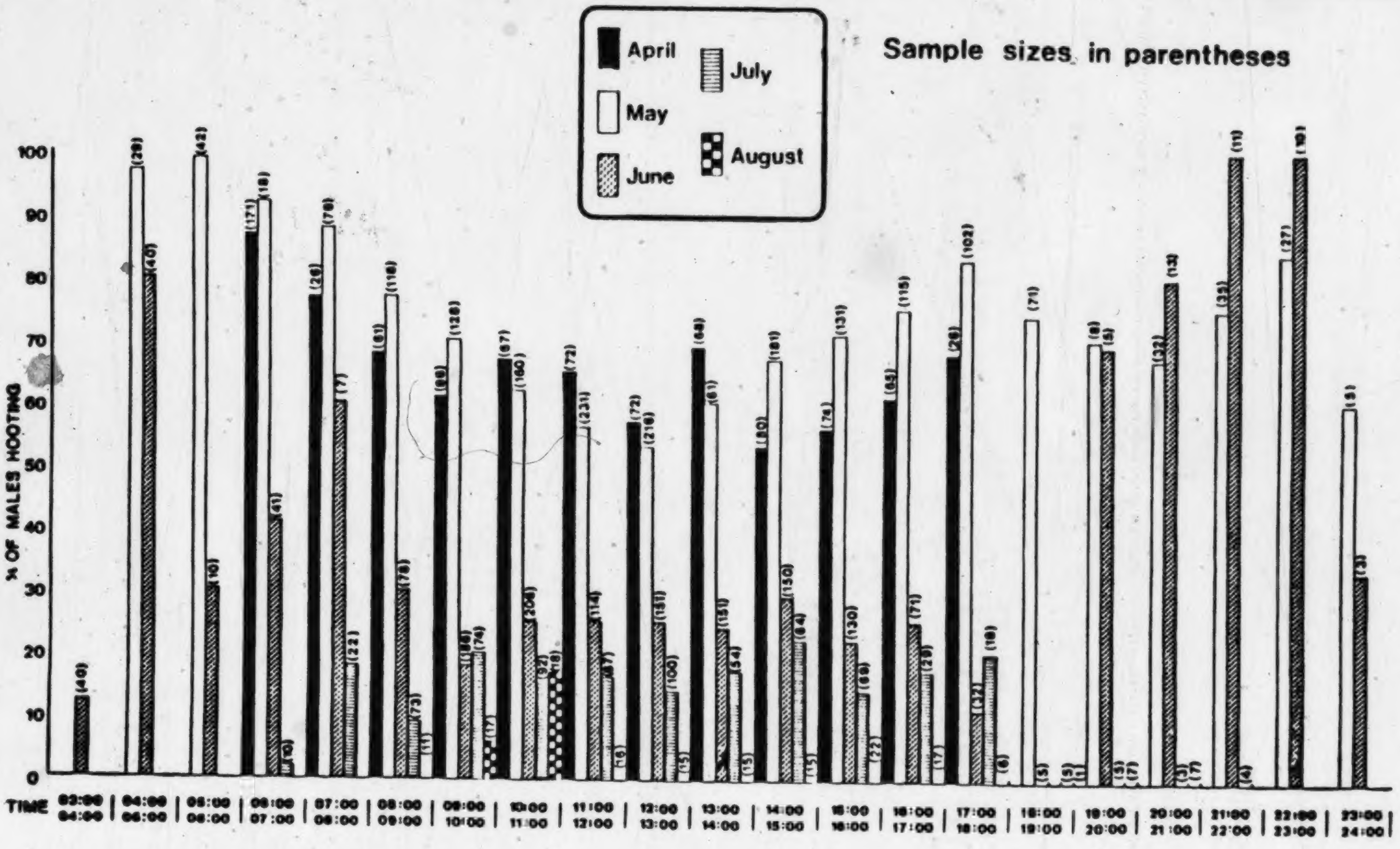

Figure 2 Percentage of Males contacted at various times of day that were Hooting, arranged by Month

LITERATURE CITED

ALEXANDER, R.D. 1974. The evolution of social behavior. Ann. Rev. Ecol. and Systematics 5: 325-384.

ARMSTRONG, E.A. 1947. Bird display and behavior: an introduction to the study of bird song. Second ed. New York, Dover.

ARMSTRONG, E.A. 1964. Lek display. pp. 431-433 in Thomson, A.L. (editor). A new dictionary of birds. McGraw-Hill, New York.

ARMSTRONG, E.A. 1973. A study of bird song. Second ed. Dover, New York.

AUBIN, E.A. 1972. Aural communication in Ruffed Grouse. Can. J. Zool. 50: 1225-1229.

BALLARD, W.B., AND R.J. ROBEL. 1974. Reproductive importance of dominant male Greater Prairie Chickens. Auk 91: 75-85.

BENDELL, J.F. 1955. Age, breeding behavior and migration of Sooty Grouse, Dendragapus obscurus fuliginosus (Ridgway). Trans. N. Am. Wildlife Conf. 20: 367-381.

BENDELL, J.F., AND P.W. ELLIOTT. 1967. Behaviour and the regulation of numbers in Blue Grouse. Can. Wildlife Rept. Ser. No. 4.

BENDELL, J.F., D.G. KING, AND D.H. MOSSOP. 1972. Removal and repopulation of Blue Grouse in a declining population. J. Wildlife Manage. 36: 1153-1165.

BENT, A.C. 1932. Life histories of North American gallinaceous birds. U.S. Natl. Mus. Bull. 126.

BLACKFORD, J.L. 1958. Territoriality and breeding behavior of a population of Blue Grouse in Montana. Condor 60: 145-158.

BLACKFORD, J.L. 1963. Further observations on the breeding behavior of a Blue Grouse population in Montana. Condor 65:485-513.

BROOKS, A.C. 1926. The display of Richardson's Grouse, with some notes on the species and subspecies of the genus Dendragapus. Auk 43: 281-287.

BROOKS, R.J., AND J.B. FALLS. 1975. Individual recognition by songs in White-throated Sparrows. III. Song features used in individual recognition. Can. J. Zool. 53: 1749-1761.

BROWN, J.L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76: 160-169.

BROWN, J.L. 1974. Alternate routes to sociality in jays with - a theory for the evolution of altruism and communal breeding. Am. Zool. 14: 63-80.

CROOK, J.H. 1964. Dominance(2). pp. 218-219 in Thomson, A.L. (editor). A new dictionary of birds. McGraw-Hill, New York.

CROOK, J.H. 1965. The adaptive significance of avian social organization. Symp. Zool. Soc. London 14: 181-218.

DORST, J. 1971. The life of birds. Vol. 1. Columbia Univ. Press, New York.

DUNHAM, D.W. 1966. Territorial and sexual behavior in the Rose-breasted Grosbeak, Pheucticus ludovicianus (L.). Z. Tierpsychol. 23: 438-451.

EDSON, J.M. 1925. The hooters of Skyline Ridge. Condor 27: 226-229.

FALLS, J.B. 1969. Functions of territorial song in the White-throated Sparrow. pp. 207-232 in Hinde, R.A. (editor). Bird vocalizations, their relation to current problems in biology and psychology. Cambridge Univ. Press, Cambridge.

FALLS, J.B., AND M.K. MC NICHOLL. in press. Neighbor-stranger discrimination by song in male Blue Grouse. Can. J. Zool.

FICKEN, M.S. 1962. Agonistic behavior and territory in the American Redstart. Auk 79: 607-632.

FISHER, J. 1954. Evolution and sociality. pp. 783. _in_ Huxley, J., and E.B. Ford (editors). Evolution as a process. George Allen & Unwin, London.

FOWLE, C.D. 1960. A study of the Blue Grouse (_Dendgrapus_ _obscurus_ (Say)) on Vancouver Island, British Columbia. Can. J. Zool. 38: 701-713.

GREENWALT, C.H. 1968. Bird song: acoustics and physiology. Smithsonian Inst. Press, Washington.

HAMERSTROM, F., AND F. HAMERSTROM. 1960. Comparability of some social displays of grouse. Proc. 12th Intern. Ornithol. Congr.: 274-293.

HARJU, H. 1974. An analysis of some aspects of the ecology of Dusky Grouse. Ph.D. thesis, Univ. Wyoming, Laramie.

HARTZLER, J.E. 1972. An analysis of Sage Grouse lek behavior. Ph.D. thesis, Univ. Montana, Missoula.

HJORTH, I. 1968. Significance of light in the initiation of morning display of the Black Grouse (_Lyurus_ _tetrix_ L.). Viltrevy 5: 39-94.

HJORTH, I. 1970. Reproductive behaviour in Tetraonidae with special reference to males. Viltrevy 7: 184-588.

HOFFMANN, R.S. 1956. Observations on a Sooty Grouse population at Sage Hen Creek, California. Condor 58: 321-337.

JOHNSGARD, P.A. 1973. Grouse and quails of North America. Univ. Nebraska Press, Lincoln.

JOHNSON, H.A. 1929. Summer notes on the Sooty Grouse of Mount Rainier. Auk 46: 291-293.

KLOPFER, P.H. 1962. Behavioral aspects of ecology. Prentice-Hall, Englewood Cliffs.

KNIGHT, T.A. 1974. A review of hearing and song in birds, with comments on the significance of song in display. Emu 74: 58.

KROODSMA, R.L. 1974. Species-recognition behavior of territorial male Rose-breasted and Black-headed grosbeaks (Pheucticus). Auk 91: 54-64.

LACK, D. 1966. Population studies of birds. Clarendon Press, Oxford.

LEIN, M.R. 1972. Territorial and courtship songs of birds. Nature 237: 48-49.

LISTER, D. 1953. Secondary song: a tentative classification. Brit. Birds 46: 139-143.

LOW, D.J. 1974. Qualities of individuals in a replacement stock of Blue Grouse. M.Sc. thesis, Univ. Brit. Columbia, Vancouver.

MARTIN, K. 1973. Breeding density and reproductive success of Robins in relation to habitat structure on logged areas of Vancouver Island, British Columbia. M.Sc. thesis, Univ. Alberta, Edmonton.

MC NICHOLL, M.K. 1973. Functions of display components in male Blue Grouse: Progress report, February 1973. Univ. Alberta, Edmonton Unpubl. report.

MC NICHOLL, M.K. 1978a. Functional aspects of display components of male Blue Grouse. in Ph.D. thesis, Univ. Alberta, Edmonton.

MC NICHOLL, M.K. 1978b. Reactions of male Blue Grouse to intrusions by observers. Appendix 2 in Ph.D. thesis, Univ. Alberta, Edmonton.

MC NICHOLL, M.K. 1978c. Territoriality of male Blue Grouse on Vancouver Island, British Columbia. in Ph.D. thesis, Univ. Alberta, Edmonton.

MORSE, D.H. 1966. The context of songs in the Yellow Warbler. Wilson

Bull. 78: 444-455.

MORSE, D.H. 1967. The contexts of songs in Black-throated Green and Blackburnian warblers. Wilson Bull. 79: 64-74.

RIPPIN, A.B., AND D.A. BOAG. 1974. Social organization among male Sharp-tailed Grouse on arenas. Can. J. Zool. 52: 591-597.

SKINNER, M.P. 1927. Richardson's Grouse in the Yellowstone Park. Wilson Bull. 39:208-214.

SMITH, W.J. 1963. Vocal communication of information in birds. Am. Nat. 97: 117-125.

SNOW, D.W. 1963. The evolution of manakin displays. Proc. 13th Intern. Ornithol. Congr.: 553-561.

STEWART, P.A. 1967. Hooting of Sitka Blue Grouse in relation to weather, season and time of day. J. Wildlife Manage. 31:28-34.

STIRLING, I., AND J.F. BENDELL. 1966. Census of Blue Grouse with recorded calls of a female. J. Wildlife Manage. 30: 184-187.

STIRLING I., AND J.F. BENDELL. 1970. The reproductive behavior of Blue Grouse. Syesis 3: 161-171.

THORPE, W.H. 1961. Bird-song. The biology of vocal communication and expression in birds. Cambridge Univ. Press, Cambridge.

THORPE, W.H. 1964. Singing. pp. 739-750 in Thomson, A.L. (editor). A new dictionary of birds. McGraw-Hill, New York.

TRIVERS, R.L. 1972. Parental investment and sexual selection. pp. 136-179 in Campbell, B. (editor). Sexual selection and the descent of man 1871-1971. Aldine Publ. Col, Chicago.

WILEY, R.H. 1974. Evolution of social organization and life-history patterns among grouse. Quart. Rev. Biol. 49: 201-226.

WILSON, E.O. 1975. Sociobiology. The new synthesis. Harvard Univ.

Press, Cambridge, Mass.

WING, L. 1946. Drumming flight in the Blue Grouse and courtship characters of the Tetraonidae. Condor 48: 145-147.

WYNNE-EDWARDS, V.C. 1965. Self-regulating systems in populations of animals. Science 147: 1543-1548.

ZWICKEL, F.C. 1972. Removal and repopulation of Blue Grouse in an increasing population. J. Wildlife Manage. 36: 1141-1152.

ZWICKEL, F.C. 1977. Local variations in the time of breeding of female Blue Grouse. Condor 79: 185-191.

ZWICKEL, F.C., AND J.F. BENDELL. 1967. Early mortality and the regulation of numbers in Blue Grouse. Can. J. Zool. 45: 817-851.

PAPER 4. Neighbor-stranger discrimination by song in Male Blue Grouse.[1]

Playback experiments demonstrated that male blue grouse can distinguish the songs (hoots) of neighbors in the correct direction from those of other males. Specific responses to playbacks differed among individuals, but each bird responded more strongly to songs of strangers than to those of neighbors. Responses to stranger playbacks were higher, while responses to neighbor playbacks were lower using Stranger-Neighbor-Stranger sequences as compared with Neighbor-Stranger-Neighbor sequences.

Introduction

An important function of song in birds is to permit individual recognition, or at least discrimination between neighbors and strangers (Falls 1969; Beer 1970). The ability to distinguish songs of neighbors from those of other individuals would have the adaptive advantage that a given male, through habituation to a neighbor near its appropriate border, would not use excessive energy in frequently attempting to chase away the neighbor (Falls 1969). This is analagous to the advantage of habituation to a potential predator nesting nearby (McNicholl 1973).

The ability of adult birds to discriminate between songs of neighbors and strangers has been demonstrated for the Australian magpie (*Gymnorhina tibicen*) (Falls 1969), great tit (*Parus major*) (Krebs 1971), stripe-backed wren (*Campylorhynchus nuchalis*) (Wiley and Wiley 1977), ovenbird (*Seiurus aurocapillus*) (Weeden and Falls 1959), yellowthroat (*Geothlypis trichas*) (Wunderle 1978), indigo bunting (*Passerina cyanea*) (Emlen 1971), field sparrow (*Spizella pusilla*) (Goldman 1973), white-throated sparrow (*Zonotrichia albicollis*) (Brooks and Falls 1975), and song sparrow (*Melospiza melodia*) (Kroodsma 1976, Harris and Lemon 1976), all passerines. Wilson (1975: 274) also lists the cardinal (*Cardinalis cardinalis*) among species in which the ability to distinguish neighbors from other individuals was tested, but Lemon (1967) in the paper cited by Wilson states that he has not investigated this aspect of cardinal behavior. Although the experiments cited above are generally interpreted as demonstrating individual recognition, Beer (1970) pointed out that the ability to distinguish the song of a neighbor from that of other individuals does not necessarily mean that individual recognition occurs. However, recent studies (Falls and Brooks 1975; Wiley and Wiley 1977), which show that neighbor-stranger discrimination is limited to the boundary of the territory shared with the neighbor in question, indicate that birds are capable of recognizing songs of individuals.

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[1] this paper is a joint contribution with J. Bruce Falls.

Experiments designed to test neighbor-stranger discrimination by song do not appear to have been conducted on non-passerine birds, although the mechanically produced drumming of the ruffed grouse (*Bonasa umbellus*) has been examined for structural differences which could enable such discrimination (Aubin 1972; Samuel *et al*. 1974). Aubin was unable to elicit sufficient drumming in response to playbacks to make an experimental comparison.

We tested 13 male blue grouse (*Dendragapus obscurus*) on Vancouver Island for ability to discriminate between the vocally produced "hooting" (Stirling and Bendell 1970), the song, of neighbors and strangers.

Materials and Methods

We conducted 26 experiments on 13 male blue grouse, all but one of which were color-banded. The unbanded bird was hooting in approximately the same place on both days, which is strong evidence that it was indeed the same bird. All but two birds were on the Comox Burn study area of Zwickel and Bendell (1972), and were subjects of detailed behavioral studies in the course of which territorial boundaries were carefully determined. One was on the experimental study area of Bendell et al. (1972), and D. King and D. Low defined the approximate boundary between this bird and its relevant neighbor for us. The other bird was in the vicinity of Upper Quinsam Lake. This bird and its neighbor were hooting in close proximity, so that we were able to define their mutual boundary with reasonable precision. Thus, in all cases individual boundaries were known.

Songs used for playback were recorded on a Nagra 3B tape recorder at 7½ ips (19.04 cms), NAB setting with a Sennheiser MKH 104 microphone on a collapsible fibreglass pole with a Sennheiser windscreen MZW 201.

Each experiment consisted of an observation period of 10 min, followed by three 15 min periods, each consisting of a 5 min playback followed by a 10 min observation period. The beginning of the first (pre-experimental) observation period was determined by JBF after MKM communicated to him via walkie-talkie that the subject was hooting and showing no indication of alarm. Tapes were played at the loudness estimated to be normal for the bird, and consisted of a continuous loop of one song followed by 10 sec of silence, an interval within the normal range of an actively singing bird (McNicholl 1978b). Playback equipment consisted of the Nagra 3B tape recorder used at the same speed and setting as for recording and a wooden speaker column in which four oval 9-in (228.6 mm) speakers plus a 4-in (101.6 mm) tweeter were mounted. Tape loops were mounted in Cousino Audio-Vendor tape cartridges.

Experiments were not performed in windy or rainy weather. Two experiments were conducted on each subject, one consisting of a playback of the appropriate neighbor's song first, then that of a "stranger," i.e., a bird he would not have heard before, and finally that of the neighbor once more (N-S-N). The closest distance between a subject and the stranger song used was 480 m. In the other experiment, the order was reversed, beginning with a playback of a stranger, then the appropriate neighbor, and finally the stranger (S-N-S). A different stranger song was used in each experiment on the same bird, and these were selected so that neighboring birds on which experiments were also performed would not have the same stranger played to them. The sequence of experiments was such that seven birds were first tested with the N-S-N sequence and six with the S-N-S sequence. All experiments were performed with the speaker column located slightly inside the territory of the subject, within 10 m of his boundary with the territory of the neighbor whose song was played. Blue grouse usually hoot at high sites within their territories, and thus subjects were uphill from us at distances ranging from 33 to 270 m. Mean territory size of 32 birds on Comox Burn was 2.11 ha (range 0.4 to 5.2) (McNicholl 1978c). All neighbor playbacks were from the "correct" direction.

Unlike passerines, which rapidly approach the speaker when song is played within their territories, male blue grouse approach intruder hooting very slowly in most cases. Although they may approach the speaker, they may not reach it within the experimental period. Thus, observations at the speaker alone give incorrect negative results. For this reason, our procedure consisted of MKM observing the bird from a hiding place close to his hooting site prior to the experiment, while JBF watched the area around the speaker column from a distance of 20 to 30 m and operated the recorder. Care was taken by both observers to remain hidden from the bird and we believe disturbance by us was minimal. MKM followed the bird when it moved, warning JBF of its approach via walkie-talkie.

Features used to measure responses of birds are detailed below.

All experiments were conducted between 16 May and 3 June 1973, a period of active hooting and territorial defence (McNicholl 1978a). The interval between two experiments on one bird was only one day in one case, 3 days in another, and 6 to 14 days in all other cases.

RESULTS

Male blue grouse do not usually appear rapidly at the speaker during playback experiments and show a variety of responses to recorded sounds, both at the speaker and away from it. Grouse responded to a playback by changes in hooting pattern and by changes in orientation, movements, and displays. Despite minor individual variations in response, we were able to construct a response scale using these features as parameters (Table 1). The scale was based on results of other experiments by MKM on inter-male behavior. The reactions of birds to dummies and live birds on which this scale is based will be presented in detail elsewhere; a brief summary follows.

A male blue grouse typically responds to the playback of a blue grouse vocalization, whether of male or female, by facing the speaker if he was initially oriented in a different direction. If he was hooting before the call was played, he will alter his hooting rate, sometimes by stopping, at least briefly. If the call played to him is hooting, as in these experiments, the bird will frequently change his hooting rate to match that of the playback, with which he will alternate. If the bird was originally over a rise from the direction of the playback, he may walk to the top of the rise, as if to hear better. Except where the playback is very close to the bird, he will not usually approach any further unless it continues for a considerable time. Changes in direction or short movements were given a low rank in the response scale. Similarly, a male may show a slight amount of white around the apteria (McNicholl 1978a). Since this is shown in response to disturbance generally, it is not considered a strong display feature. If hooting is played at a time of the year when the bird will respond to sounds made by "intruders," he will typically stop hooting briefly, often show some display feature(s), and move slowly towards the sound, stopping frequently to hoot en route. He may remain in partial display or show no display features as he approaches the source of the sound. Partial display refers to lateral apteria partially flared, combs flared but not red, and tail raised but not fanned. At close range he will show Full Display, i.e. his lateral apteria or "air sacs" will be fully flared, his tail up and fanned, and his combs flared and often red. On seeing a male dummy or live male, the bird may then growl or show aggressive postures, with neck stretched and body sleek (see Stirling and Bendell 1970), or both, and attack. Full display appears to be a general response given while approaching any intruding grouse, male or female, presumably announcing the presence of a territorial male, whereas aggressive postures and growling are given only as a more intense maleexpulsion response.

Table 2 shows the results of our 13 pairs of experiments. Clearly, there was a greater response to hooting of strangers than to those of appropriate neighbors (P<0.0003 Wilcoxon Matched-Pairs Signed-Rank Test (Siegel 1956)). Thus, by combining several features of response to playback, we have demonstrated stranger-neighbor discrimination in males of this species.

The results shown in Table 2 also indicate more subtle differences resulting from order of presentation. Overall response to playbacks was stronger in S-N-S experiments than in N-S-N experiments, since the former had higher total scores in 12 of the 13 pairs of experiments. The Wilcoxon Matched-Pairs Signed-Rank Test indicates that S scores (S of N-S-N vs S of S-N-S) were greatest in the S-N-S experiments (P<0.01, one-tailed test). Responses to the N's (N of N-S-N vs. N of S-N-S) were stronger in the N-S-N experiments, although with a lower probability value (.05>P<0.025).

The following sections briefly document responses in terms of the specific parameters used in our rating scale.

Orientation

Changes in orientation of experimental birds following playback are summarized in Table 3. The data show a high tendency for birds to face the source of the new sound. Many then revert to their original direction during periods of silence, hooting with a real neighbor during these intervals. The higher number of incidents in which the bird remained facing the speaker in silent portions of S-N-S experiments than in those of N-S-N experiments (5:1) is consistent with the finding that responses tend to be stronger during the former experiments. However, changes in orientation seem to be a low key response, given to any new source of hooting.

Changes in Hooting Rate

Responses in hooting rate were variable, with no consistent pattern emerging. Initially a bird usually altered his hooting to match that of the speaker. This was continued throughout the playback in most cases, but some birds stopped singing. No birds reverted to the original hooting rate while the playback was still playing. Chi-squared values for comparisons of intervals between songs before and during playback did not show a clear difference because drastic initial changes were often offset by further changes during the experiment. Changes in hooting rate seemed a low key response though other experiments indicate that it is stronger than a change in orientation.

Displays

The amount of display by an individual varied markedly, but a given bird tended to give a stronger display towards S than N hooting (Table 4). In some experiments, no postural responses were shown to playbacks. In one experiment, Full Display was assumed in response to both S and second N playbacks, but the latter appeared to be an artifact of disturbance, rather than a response to the tapes, as the bird displayed when he came into a position where he could see the observer.

Movements

Table 5 summarizes comparative distances moved by birds in response to N and S playbacks in the two experimental situations. As with other features examined, movements varied considerably among birds. Three movements included flight, all others walking only. In two cases birds moved back to their original hooting locations on hearing the second N playback after having approached the speaker during the S playback (both N-S-N experiments). In one experiment, the bird flew to the speaker on the first N, perhaps because his initial location was close (33 m) to the speaker. Birds tended to move sooner and further to S playbacks than to N playbacks. Movement alone is not always a good measure of response, since the bird may cover the total distance on the first playback. Nevertheless, movements did show a clear differential response when comparisons could be made.

Discussion

The results documented above provide strong evidence that male blue grouse can distinguish songs of neighbors from those of other males, as has previously been shown for other species of birds. No previous evidence for such discrimination appears to have been published for non-passerine birds, although individual recognition between adults and young is well known, expecially in larids (see references in reviews by Falls 1969 and Beer 1970). Samuel _et al_. (1974) and Aubin (1972) examined the drumming of ruffed grouse for structural differences that could enable individual recognition. Their results are somewhat conflicting in that of 19 variables analyzed by Samuel _et al_. (1974), none was considered a practical and rapid method for individual recognition. Nevertheless, Aubin (1972) found differences in two parameters of drumming that could allow individual recognition.

In the present study, total response was greater in the S-N-S experimental sequence than in the N-S-N sequence. This resulted from a greater response to S during S-N-S experiments. In fact, responses to N in S-N-S series were weaker than in the N-S-N series. This suggests that initial exposure to a stranger's song increases a bird's tendency to discriminate. By contrast, in N-S-N sequences responses to N are relatively stronger while those to S are weaker than in S-N-S experiments. Discrimination, though clearly shown, is reduced in the former as compared to the latter case. It has been suggested elsewhere that habituation to N songs may be responsible for N-S discrimination (Falls 1969; Petrinovich and Peeke 1973; Armstrong 1973). Perhaps, prior exposure to a song to which the bird is already habituated reduces its tendency to discriminate. Since responses are strongest to S songs in S-N-S sequences and strongest to N songs in N-S-N sequences, it may simply be that response is enhanced by the song heard first in the series.

The individual variability in response shown by male blue grouse shows the difficulty in attempting to demonstrate neighbor-stranger discrimination by using only one variable as a response measure. However, by comparing total responses of an individual bird in the two experimental situations, it was possible to compare his response to different stimuli, and thus demonstrate his discriminatory ability. A similar scaling of responses was used by Emlen (1971) and Emlen _et al_. (1975).

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Table 1

Response scale for male blue grouse reacting to playbacks of hooting.

Rating	Criteria
0	No reaction. Bird continues hooting or remains silent as before. No movement or indication of display.
1	Faces speaker and/or alternates hooting with that of the speaker with no change in hooting rate and no further response.
2	Stops hooting or significantly alters hooting pattern. Any movement is confined to one short movement sufficient only to allow him to reach the crest of a hill. No display, although he may show some white around the lateral apteria.
3	Continuous or repeated movement towards the speaker and/or partial display shown.
4	Movement towards speaker in full display or flight followed by full display, or full display by bird already at speaker.
5	Aggressive posture and/or growl.

Table 2

Summary of responses to playbacks, based on response scale of Table 1.

Experimental bird	Order of Presentation										Higher total
	N-S-N*					S-N-S*					
	N	S	N	$\overline{N}$	T'	S	N	S	$\overline{S}$	T'	
1	1	2	1	1	4	3	1	3	3	7	S-N-S
2	0	1	0	0	1	5	1	5	5	11	S-N-S
3	2	3	1	1.5	6	5	1	5	5	11	S-N-S
4	2	4	1	1.5	7	4	1	5	4.5	10	S-N-S
5	1	4	1	1	6	4	1	5	4.5	10	S-N-S
6	2	3	2	2	7	4	1	5	4.5	10	S-N-S
7	1	3	1	1	5	4	1	4	4	9	S-N-S
8	2	3	1	1.5	6	4	1	4	4	9	S-N-S
9	1	4	4	2.5	9	4	1	5	4.5	10	S-N-S
10	2	3	1	1.5	6	4	1	4	4	9	S-N-S
11	4	5	4	4	13	4	1	3	3.5	8	N-S-N
12	1	3	1	1	5	3	1	4	3.5	8	S-N-S
13	1	4	0	0.5	5	4	2	4	4	10	S-N-S
Total	20	42	18	19		52	14	56	54		

' Total response in experiment

* N = song of neighbor from correct direction, S = song of stranger

Table 3

Changes in orientation of experimental birds following playback of hooting.

Response	N-S-N*	S-N-S*
Away from speaker in all silent periods, towards speaker in all playbacks	10	8
Towards speaker on S only	1	0
Towards speaker on S and first N only	1	0
Towards speaker throughout experiment	1	5

* N = song of neighbor from correct direction, S = song of stranger

Table 4

Displays of male blue grouse to playbacks of hooting.

Display score*	N-S-N*		S-N-S*	
	N	S	S	N
0	10	2	0	13
1	1	1	0	0
2	0	5	1	0
3	2'	4	6	0
4	0	1	6	0

* 0 = no display; 1 = slight display; 2 = partial display; 3 = full display; 4 = aggression; N = song of neighbor from correct direction; S = song of stranger

' one bird displayed to observer

Table 5

Distances moved by male blue grouse in response to playbacks of hooting.

Greater distance moved	N-S-N*	S-N-S*
$S > \overline{N}$ or $\overline{S} > N$	11	11
$N = S$ or $S = N$	2	2
$S < \overline{N}$ or $\overline{S} < N$	0	0

N = song of neighbor from correct direction; S = song of stranger

ARMSTRONG, E.A. 1973. A study of bird song. 2nd ed. Dover, New York.

AUBIN, A.E. 1972. Aural communication in ruffed grouse. Can. J. Zool. 50: 1225-1229.

BEER, C.G. 1970. Individual recognition of voice in the social behavior of birds. Adv. Study Behav. 3: 27-74.

BENDELL, J.F., D.G. KING, and D.H. MOSSOP. 1972. Removal and repopulation of blue grouse in a declining population. J. Wildlife Manage. 36: 1153-1165.

BROOKS, R.J., and J.B. FALLS. 1975. Individual recognition by song in white-throated sparrows. I. Discrimination of songs of neighbors and strangers. Can. J. Zool. 53: 879-888.

EMLEN, S.T. 1971. The role of song in individual recognition in the indigo bunting. Z. Tierpsychol. 28: 241-246.

EMLEN, S.T., J.R. RISING, and W.L. THOMPSON. 1975. A behavioral and morphological study of sympatry in the indigo and lazuli buntings of the Great Plains. Wilson Bull. 87: 145-179.

FALLS, J.B. 1969. Functions of territorial song in the white-throated sparrow. pp. 207-232 in HINDE, R.A. (Ed.). Bird vocalizations. Cambridge Univ. Press, Cambridge.

FALLS, J.B., and R.J. BROOKS. 1975. Individual recognition by song in white-throated sparrows. II. Effects of location. Can. J. Zool. 53: 1412-1420.

GOLDMAN, P. 1973. Song recognition by field sparrows. Auk 90: 106-113.

HARRIS, M.A., and R.E. LEMON. 1976. Responses of male song sparrows *Melospiza melodia* to neighboring and non-neighboring individuals. Ibis 118: 421-424.

KREBS, J.R. 1971. Territory and breeding density in the great tit, Parus major L. Ecology 52: 2-22.

KROODSMA, D.E. 1976. The effect of large song repertoires on neighbor "recognition" in male song sparrows. Condor 78: 97-99.

LEMON, R.E. 1967. The response of cardinals to songs of different dialects. An. Behav. 15: 538-545.

MC NICHOLL, M.K. 1973. Habituation of aggressive responses to avian predators by terns. Auk 90: 902-904.

MC NICHOLL, M.K. 1978a. Functional aspects of some display components of male blue grouse. in Ph.D. thesis, Univ. Alberta, Ecmonton.

MC NICHOLL, M.K. 1978b. Vocal communication among male blue grouse. in Ph.D. thesis, Univ. Alberta, Edmonton.

MC NICHOLL, M.K. 1978c. Territories of male blue grouse on Vancouver Island. in Ph.D. thesis, Univ. Alberta, Edmonton.

PETRINOVICH, L., and H.V.S. PEEKE. 1973. Habituation to territorial song in the white-crowned sparrow (Zonotrichia leucophrys). Behav. Biol. 8: 743-748.

SAMUEL, D.E., D.R. BEIGHTOL, and C.W. BRAIN. 1974. Analysis of the drums of ruffed grouse. Auk 91: 507-516.

SIEGEL, R. 1956. Non parametric statistics for the behavioral sciences. McGraw-Hill Book Co., Inc., New York.

STIRLING, I., and J.F. BENDELL. 1970. The reproductive behaviour of blue grouse. Syesis 3: 161-171.

WEEDEN, J.S., and J.B. FALLS. 1959. Differential responses of male ovenbirds to recorded songs of neighboring and more distant individuals. Auk 76: 343-351.

WILEY, R.H., and M.S. WILEY. 1977. Recognition of 'neighbors' duets by stripe-backed wrens Campylorhynchus nuchalis. Behaviour 62: 10-34.

WILSON, E.O. 1975. Sociobiology, the new synthesis. Harvard Univ. Press, Cambridge.

WUNDERLE, J.M., JR. 1978. Differential response of territorial yellowthroats to the songs of neighbors and non-neighbors. Auk 95: 389-395.

ZWICKEL, F.C., and J.F. BENDELL. 1972. Blue grouse, habitat, and populations. Proc. XV Internatl. Ornithol. Cong.: 150-169.

PAPER 5. TERRITORIES OF MALE BLUE GROUSE ON VANCOUVER ISLAND

ABSTRACT. Territory size of male Blue Grouse varied widely and was not obviously related to any one extrinsic parameter, but may be determined by a combination of extrinsic and intrinsic factors. Once established, the territory of a given bird rarely changed, but successors did not occupy areas identical to those of predecessors. There was a strong tendency to sing ("hoot") from a few specific sites within the territory.

From 1971 to 1974 I studied the social systems of male Blue Grouse (*Dendragapus obscurus*) on Vancouver Island, British Columbia. Several studies have shown that males are generally territorial on the breeding grounds (e.g. Bendell 1955; Hoffman 1956; Blackford 1958, 1963; Boag 1966; Bendell and Elliott 1967; Martinka 1972). Thus, part of my study concerned the study of territory. In this paper, I examine some characteristics of territories, stability of territories among years, stability of territorial space with changes in resident males, and use of space within territories.

METHODS

The study area. - Grouse were studied on Comox Burn (Zwickel and Bendell 1972), approximately 19 km northwest of Courtenay, British Columbia. The area is described in more detail by Zwickel (1972) and Martin (1973), and portions particularly relevent to this study below.

Size and characteristics of territories. - Size of territory was determined for 33 males all of which were color banded. Sightings by me and other observers were plotted on a grid map and lines drawn around the enclosed points to define individual territories. A territory was considered to be a spatial unit of exclusive use by one adult male. For purposes of defining territory boundaries, all points at which a bird was seen were presumed to be within his territory, i.e. an area from which he would exclude other males. Sightings of two birds singing close to a mutual boundary and aggressive responses to playbacks of singing helped define precise boundaries, and confirmed the assumption that these points were within an actual territory. All points were used in drawing enclosing lines, and the coordinates of these points put in a computer program to determine units of area within each territory. Points far from known territories were excluded as presumed errors in identification, or, in a few cases when birds were known to have been off their territories, either during first sightings in the spring when they were presumably en route to territories, or in one case during a playback experiment. The maximum number of points removed for any one bird was two (of a sample size for this bird of 71).

The number of prominent ridges, hills, or other high spots which stood conspicuously above surroundings was noted for each territory. The spatial relationship of these, plus gullies, streams, roads and major bogs was defined. Density of vegetation was determined according to the classification of Bendell and Elliott (1966, 1967).

Stability of territory among years and of territorial space used by successive birds. - In order to evaluate stability of territories of specific males among years, I plotted all sightings for each year an individual bird was present and compared resulting territories by amount of overlap and nonoverlap. Territories of successive males were drawn on transparent paper and compared with territories of the original birds.

Use of space within the territory. - The use of space within each territory was determined through examination of all sightings by all observers. Locations were compared to known hooting (singing) sites.

RESULTS

Characteristics of territories. - Figures 1 to 3 depict approximate territorial boundaries of principal males studied in 1972, 1973 and 1974, including three unbanded birds whose territories were not used in calculations. There was occasional slight overlap of territories in a few cases each year, but most territories were exclusive. The maps exaggerate the overlap somewhat, as overlap zones were rarely used by both birds at the same time, and territories of some replacement birds are shown in the same year as the bird replaced. For example, in 1973 male 1753 was present early in the season and only male 4231 occupied the territory later. The unbanded bird shown on the territory of male 1865 in 1974 (Figure 3) did, in fact, occupy the territory concurrently with 1865. However, 1865 was lame in 1974 and presumably could not expel the intruder.

The number of prominent ridges, hills, or other high spots in the territories ranged from three to seven, with a mean of 4.2 and mode of three to four (11 cases of 3 and 11 cases of 4). In one case a regularly used "high spot" in an area of relatively low ground was a dead snag partially fallen and parallel to the slope on which it was situated. All others were ridges, hills or prominent knolls. Even on these, a bird sometimes selected an even higher perch, such as a stump, from which to sing.

Vegetation density of 34 territories (of 33 males, one with two territories) ranged from "very open" to very dense," but with some "very open" and "open" spaces on all territories (Table 1). The rapid growth of vegetation on Comox Burn caused a marked rise in denser catagories over the years of study.

Animals often use natural lines in the environment as territorial boundaries (Leyhausen 1971: Brown and Green 1976). This was sometimes apparent for male Blue Grouse on Comox Burn, where boundaries were often along ridges, major streams, or bogs, but some territories crossed such features, and roads appeared to be irrelavent as territorial boundaries (Table 2).

Size of territories. - Accuracy of determination of size of territories increases with number of observations up to a point where further observations do not contribute to an increase in size (Odum and Kuenzler 1955; Stenger and Falls 1959; Bendell and Elliott 1967; and others). In the 34 territories I measured, this point was reached at 5 to 24 observations ($\overline{x} = 11.9$). Numbers of points available ranged from 6 to 71, with only six territories having less than the average number of points needed. Only one of these six appeared to be inadequately measured.

Mean size of territory was 2.20 ha (SE = 0.38), with extremes between 0.01 and 7.0 ha (Table 3). The smallest seemed to be inaccurate, and the largest included two sightings which may have been before the bird was on territory. Excluding these two values, the range is 0.4 to 5.2 ha (mean = 2.11, SE = 0.26).

Since only one bird expanded its territory during the years of my study, age seemed unrelated to territory size, a conclusion also reached by Bendell and Elliott (1967). Moreover, a comparison of territory sizes ranked from largest to smallest with birds of known age showed no pattern (Table 4). For example, three birds of one age occupied the sixth, seventh, and fifteenth largest territories, and three of another age occupied the fifth, tenth and eighteenth largest territories. Similarly territory size did not appear to be related to "hooting dominance" (McNicholl 1978a), hooting persistence, amount of "openness," or number of hooting sites within a territory (Table 4).

Stability of territories among years. - Once territory has been established, males appear to return to the same territory in subsequent years (Bendell 1955; Blackford 1963; Boag 1966; Bendell and Elliott 1967; Mussehl cited by Hjorth 1970; Martinka 1972; Harju 1974). This generalization was true of all grouse I studied for more than one year, with the exception of male 2801. This bird shifted from his 1971 territory to a nearby territory in 1972 (Fig. 1). However, during 1972 he disappeared earlier than is usual for adult males from this population, and his shift may have been caused by an inability to defend his original territory (on which an unbanded bird was hooting in 1972). In addition, I recorded two minor territorial shifts; all other territories remained virtually identical from year to year. In 1972, males 2688 and 5624 hooted at different times from an identical hill, my only case of prolonged territorial overlap (Fig. 1). In 1973, male 5624 ceased using this hill, but extended his territory to encompass a major portion of that of male 3766, who did not appear that year, as well as previously vacant land between their territories (Fig. 2). Male 1754 occupied his full territory of previous years early in 1974, but then vacated a frequently used hooting site when male 6459, a new bird, moved in. This may have been the beginning of the decline of 1754, as he was at least ten years old and did not return in 1975.

Use of space within a territory by a given male. - Male Blue Grouse spent a substantial amount of time singing at three to seven (usually three to four) regular hooting spots (McNicholl 1978a). Even when not singing these birds were found within 15 m of these sites over 80 per cent of the time (Table 5). Most observations away from these sites involved encounters by other observers searching with dogs, which may have caused the bird to run some distance before being seen. Others involve birds sheltering or feeding in marshy spots on hot days, and birds which I followed from one hooting spot to another. None of these observations involved hooting birds.

Stability of territorial space when resident changes. - Although replacement males occupied territories similar to those of original males, territorial boundaries were not the same and more than one bird might fill a vacated area (Table 6: see especially replacement of males 3766 and 4803).

DISCUSSION

Characteristics of territories. - As in this study, Bendell and Elliott (1967) also report a very small degree of overlap of territories in another Vancouver Island population of *D. o. fuliginosis*, and Boag (1966) found no territorial overlap in a population of *D. o. richardsonii* in Alberta.

Blackford (1958) mentioned high ridges in territories of Blue Grouse, but did not stress their importance. Boag (1966) considered topography as especially important in the selection of territories and noted that at low densities only higher sites were occupied. Similarly, Bendell and Elliott (1966, 1967) found that males tended to select "heights of land" within open areas as characteristic features of territories. On the other hand, Donaldson (1973) found no relationship between number of hooting males per 100 acres and number of peaks per 100 acres on Prevost Island, B.C., but she did not state whether all such peaks were within territories. I found that males used such high spots almost exclusively while singing, though not necessarily at the highest points. Such heights appear to be important as conspicuous singing posts from which males can "announce" their continued presence.

Bendell and Elliott (1966, 1967) found a preference for open areas by territorial males on Vancouver Island. Martinka (1972) mentioned the importance of open areas on territories in Montana, with shrub cover less plentiful in areas used for territories than in areas not used for territories. Boag (1966) found that canopy cover of approximately 50% constituted the most "acceptable" areas for territories, with less dense and more dense areas less favored, a finding consistent with earlier studies cited by him. Martinka (1972) felt that clumps of coniferous trees and open spaces were both important components of territories. On Comox Burn, most of the territories I studied were initially in areas with considerable open space, but these diminished each year, with each bird occupying a more densely vegetated territory merely by not vacating his established territory. However, even in the most dense territories there were open spaces, and singing posts were always adjacent to open spaces. Male Blue Grouse approach hens during courtship in a highly visual display (McNicholl 1978b), and I agree with Bendell and Elliott (1967) that such open spaces are probably important for courtship activity. If hens approach singing males, as suggested by playback experiments (McNicholl 1978b), singing posts would best be located near such places. Bent (1932), in summarizing early accounts, indicated that Blue Grouse are found in habitat ranging from open meadow to dense forest, but the latter may include open spaces.

Size of territory. - My values for territory size are similar to those of Bendell and Elliott (1967) who report a range in size from 0.4 to 2.8 ha for the same race.

Various parameters have been suggested as determinants of territory size in birds and other animals. Bendell and Elliott (1967), Boag (fide Hjorth 1970) and Martinka (1972) noted larger territories in sparse populations of Blue Grouse than in denser populations, as is also known for several passerines (e.g. Anderson and Anderson 1973). In this study, however, I found as much variation in territory size within one population as they did between populations. In one case two males occupied a total area slightly less than the territory of one previous occupant (male 4803 with a territory of 3.5 ha was replaced with males 6470 and 6517, with combined territories totalling 2.9 ha). In another case, male 5624 expanded into part of the territory of a previous occupant. Thus, in one case a doubling of the males on a territory space occurred, with smaller territories resulting, while in another case a territory expanded with the elimination of one male. If one assumes that the increase in territorial males in the first case and lack of additional males in the second case both represent replacement birds, then these cases are consistent with the above proposed relationship between territory size and populations, but the data are too few to draw definite conclusions.

Bergerud and Hemus (1975) found that males from different populations on Vancouver Island established territories of different sizes when transplanted to a smaller island, and suggested that these differences were genetic. They also suggested a relationship between these differences in territory size and aggression, as measured by an "arena test." If aggression is correlated with "hooting dominance", no such relationship between size of territory and aggressiveness was found in my study population: at least no relationship appears to exist between size of territory and hooting dominance (Table 4). Persistence of singing has been correlated with large territories in birds (Conder 1948; Armstrong 1973) and frogs (Whitney and Krebs 1975), even to the extent of vigorous singers taking over territories and mates of less vigorous singers (Armstrong 1955). However, a comparison of size of territory to ranking in hooting persistence (Table 4) showed no such correlation in my population.

Bendell and Elliott (1967) found a greater tendency to more uniform distribution of territorial males in open cover than in dense cover, and Boag (1966) found a strong correlation between size of territory and size of clumps of cover in Alberta. However, I found no relationship between "openness" and size of territory in my population, nor a close relationship to number of hooting sites within the territory (Table 4) or age (Table 4). I suspect size of territory is determined by a complex array of intrinsic and extrinsic factors, including population density, vegetative cover, hooting persistence of neighbors, topography, and possibly genetics.

The function or adaptive significance of such large territories is problematical. The foods of Blue Grouse are largely of plant species found in abundance on Comox Burn (see Zwickel 1972; Zwickel and Bendell 1972). Males take no part in nest defence or care of young (Johnsgard

1973), and most nests are not even within the territories of adult males (Zwickel per. comm.). In terms of resources used, these territories seem unnecessarily large. Beer et al. (1956) suggested that the biological value of such large territories could be in securing mating functions. Similarly, Verner (1977) has recently argued that natural selection favors individuals which defend "super territories," larger than necessary for sufficient resources, by ensuring that these individuals contribute more to the genepool than less aggressive conspecifics. If females select males with which to mate on the basis of their holding territories, and perhaps those of highest hooting dominance as suggested elsewhere (McNicholl 1978a), territories of male Blue Grouse could be examples of Verner's (1977) "super territories." Further work is needed to test this possibility.

Stability of the territory of a given male from year to year. -High fidelity to a territory as found for Blue Grouse has also been noted for other grouse (e.g. Thompson 1891; Boag 1976; Hjorth 1970: 500), passerines (e.g. Nice 1943; Lack 1965; Anderson and Anderson 1973), and other species of birds, especially in stable habitats (McNicholl 1975). The adaptive significance of such fidelity is usually stated to be in familiarity with the local environment, thus ensuring greater chance of escape from predators, greater ability to locate food, etc. In Blue Grouse, such fidelity could play an important role in the social system. Since males are capable of distinguishing songs of neighbors from those of other individuals (Falls and McNicholl in press) and males sing in social groups (McNicholl 1978a), fidelity to territory would ensure maintenance of an established social system, and avoid the need to establish new relationships with neighbors each year.

Territorial shifts have also been noted by others. Blackford (1963) noted a shift in one bird's territory between two years, but without supporting evidence, and Harju (1974: 35) stated that slight changes in territorial boundaries of Blue Grouse occur, but gave no details. Such shifts appear to be rare, and may reflect inability to hold a territory.

Use of space within a territory by a given male. - Bendell (1955), Bendell and Elliott (1967), Blackford (1963), Rogers (cited by Johnsgard 1973), Harju (1974), and Bergerud and Hemus (1975) have all noted the frequent use of precise spots within territories of male Blue Grouse, especially for singing. Rogers (cited by Johnsgard 1973) noted a range of two to eleven such sites within territories, whereas I found three to seven in my population. This fidelity to specific sites within the territory could be important in singing groups, each bird within a group regularly singing from predictable places, and thus informing his neighbors that he remains on the same territory and is not attempting to encroach on the neighbor's territory.

Stability of territorial space when resident male changes. - Bendell and Elliott (1966, 1967) suggested that a territory is perpetuated by replacement male Blue Grouse. Boag (cited by Hjorth 1970) also noted that territories remain the same over several years, even with a change of occupant. Martinka (1972) found that some territories were occupied continuously by the same bird or by different birds whereas others were occupied only intermittently. In my study, males did not occupy identical territories when one or more bird(s) replaced another, although they did occupy the same general areas. This indicates that the ground occupied was not in itself the important parameter in location of territory, but rather the space within the social system. Much of the vacant ground between territories (Figs. 1 to 3) seemed little different from that occupied by territorial birds, and indeed was shown to be suitable to the birds by subsequent occupation by new birds. At the same time, portions of old territories sometimes became vacant when one bird was replaced by another.

Territories in the social system of male Blue Grouse. - Two social systems are commonly found in grouse: solitarily territorial and the lek, or communal system (Wing 1946; Hamerstrom and Hamerstrom 1960; Hjorth 1970; Hartzler 1972; Johnsgard 1973; Ballard and Robel 1974; Rippin and Boag 1974; Wiley 1974). The Blue Grouse is traditionally considered to be solitarily territorial, with territoriality inferred from their pattern of dispersion on the breeding grounds (Bendell and Elliott 1967; Boag 1966; Martinka 1972; and others). Experiments showing that males respond aggressively to visual displays and songs of other males (McNicholl 1978b) indicate that males do indeed exclude other adult male conspecifics from the area they occupy, and thus are territorial by the definition of Pitelka (1959).

Bendell and Elliott (1967) stated that territories of male Blue Grouse readily fit Nice's (1941) "mating and display" type, but since these territories are used for both feeding and mating by males with no apparent relevance to location of nests or young, they cannot readily be fitted into the classifications of territories proposed by Mayr (1935), Nice (1941), or Hinde (1956). They do technically fit into Armstrong's (1947) type Eb territory, i.e. "Feeding. In the breeding season but not connected with rearing young," but this classification implies this is primarily a feeding territory, which is unlikely. As mentioned above, these territories appear to fit Verner's (1977) concept of "super territories."

Some observers claim that communal displays occur in inland races of Blue Grouse (Wing 1946; Blackford 1958, 1963; Harju 1974). Although Hjorth (1970) characterized Blue Grouse as a polygamous species with solitary display, their vocal behavior appears to be socially oriented, with males singing in social groups (McNicholl 1978a). Thus, the social system of Blue Grouse is solitarily territorial among males, but with social elements of lek species, possibly even including dominance (McNicholl 1978a). One advantage suggested for lek behavior is that females may select males who are genetically most fit, with dominance being an indication of genetic superiority (Trivers 1972). In such a system the few males which effect most matings must mate quickly in order to avoid interference (Trivers 1972). If females can detect "fit" males through singing, they could select "superior" males with which to mate in a territorial species with singing dominance, and could mate with such males without interference.

Harju (1974) believed that adult males establish new territories prior to arrival of females, but on my study area most males present before the arrival of females held territories in previous years. In five cases, males present early in the spring disappeared shortly after females and yearlings arrived, and in another a male lost part of his territory at this time (see Table 6). The bird which occupied the remainder of the territory of the latter was a banded two year old which had been seen nearby as a yearling. I also have seven records of territories which appeared to be established after females arrive. Thus, territorial establishment does not appear to occur prior to arrival of females, but rather coincident or soon after this period.

Removal experiments and rapid replacement of birds which die indicate that a "surplus" or group of nonterritorial birds exists in the Vancouver Island populations (Bendell et al. 1972; Zwickel 1972). Observations during playback experiments using female calls, and other incidental observations, suggest that these birds remain on or near territories of resident males. Such birds are likely watching for a vacancy and will not likely challenge the resident unless he appears weak or injured. On rare occasions (see birds 1865 and 4803 in Table 6), these birds may even sing on the territory of a weak male before the latter disappears. The fact that these birds, which banding has shown to be yearlings or two year old birds in some cases (F.C. Zwickel files), do not establish territories in unoccupied areas, but quickly fill in positions of lost birds, suggests that entry in an existing social system is preferable to attempting to establish new social groups.

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TABLE 1. Density of vegetation on 34 territories of Blue Grouse.

Density of Vegetation*	Number of territories
Very open to open	8
Very open to dense	15
Very open to very dense	1
Open to dense	7
Open only	2
Open to very dense	1

Predominate cover type*	Number of territories
Very open	2
Open	24
Dense	8
Very Dense	0

Percent Cover types* on territories by year:

Cover type	1971	1972	1973	1974
Very open	25.0	24.7	7.8	2.5
Open	64.4	66.8	74.7	62.4
Dense	10.6	8.5	17.5	33.1
Very Dense	0.0	0.0	0.0	0.4

* Classification of Bendell and Elliott (1966, 1967)

TABLE 2. Territorial boundaries in relation to environmental features.

Territory-feature relationship	Number of Territories (N=34)
One or more ridge(s) form boundary	24
One or more ridge(s) traverse boundary	26
One or more stream(s) form boundary	10
One or more stream(s) traverse territory	7
One or more bog(s) form boundary	8
One or more bog(s) traverse territory	2
One or more road(s) form boundary	2
One or more road(s) traverse territory	22

TABLE 3. Size of territories of Blue Grouse on Comox Burn.

Size of Territory (ha.)	Number of Territories
0.01-0.9	8
1.0-1.9	8
2.0-2.9	10
3.0-3.9	5
4.0-4.9	1
5.0-5.9	1
6.0-6.9	0
7.0	1

TABLE 4. Size of Territory compared to several parameters.

Age vs. size of territory: simple correlation, $r = 0.76$, not significant

territory size ranks vs. hooting dominance:

dominant: 2, 3, 4, 7, 11, 16, 19

intermediate: 5, 10, 12, 13, 14, 17, 20, 24, 25, 26, 28

subordinate: 1, 6, 15, 18, 20, 23, 27, 29

territory size vs. hooting persistence: Spearman rank correlation coefficient (Zar 1974): $rs = -0.24$, not significant.

territory size ranks vs. vegetation density

very open to open: 7, 11, 15, 17, 18, 21, 32, 34

very open to dense: 2, 3, 4, 5, 6, 8, 12, 13, 19, 23, 24, 25, 26, 28, 29

very open to very dense: 1

open to dense: 9, 10, 14, 16, 22, 30, 31

open only: 20, 33

open to very dense: 27

territory size ranks vs. number of hooting sites:

3 sites: 1, 6, 10, 16, 21, 24, 26, 30, 31, 34

4 sites: 3, 8, 9, 15, 17, 20, 22, 23, 27, 28, 29, 32

5 sites: 5, 7, 11, 12, 13, 14, 19, 25, 33

6 sites: 4, 18

7 sites: 2

TABLE 5. Location of non-singing males in relation to regular singing posts*

Where found	% of searches	% of all males
15 m or less from a hooting post	80.2 - 95.1 %	84 %
found more than 15 m from hooting post	4.2 - 18.5 %	11 %
could not be found	0.0 - 18.1 %	5 %

* based on records of 33 banded and 3 unbanded regularly worked males between periods of first and last sightings for year.

TABLE 6. Changes in use of territory space with changes in residents.

Original male	New pattern of occupancy
1313	In 1974, 6525 occupied part of this territory and some previously unoccupied area.
1753	1753 was present early in 1973, then disappeared. 4231 used about two-thirds of this territory plus previously unoccupied area.
1880	In 1974, 6239 used a small portion of this territory.
2801	His first territory was occupied after 1971 by an unbanded bird, whose territory only partially overlapped that of 2801. In 1973 and 1974, 5664 occupied a territory of 2801 and part of the former territory of 3766.
3766	When 3766 disappeared, 5664 occupied part of his territory and 5624 expanded into the rest of it.
4803	In 1973 an unbanded bird began hooting on his territory shortly before 4803 disappeared. F.C. Zwickel banded the newcomer as 6517. In 1974, 6517 and 6470 each occupied portions of the old territory of 4803 plus previously vacant area.
4817	6459 occupied most, but not all of the former territory of 4817 in 1974, and encroached on that of 1754.
1865	A portion of his territory was occupied simultaneously with an unbanded bird after 1865 became lame in 1974.

Figure 1. Territorial boundaries of male Blue Grouse studied in 1972. 2801-a indicates the 1971 territory of male 2801 in order to indicate its spatial relationship with the 1972 territory (2801-b). Territories of unbanded birds are approximate.

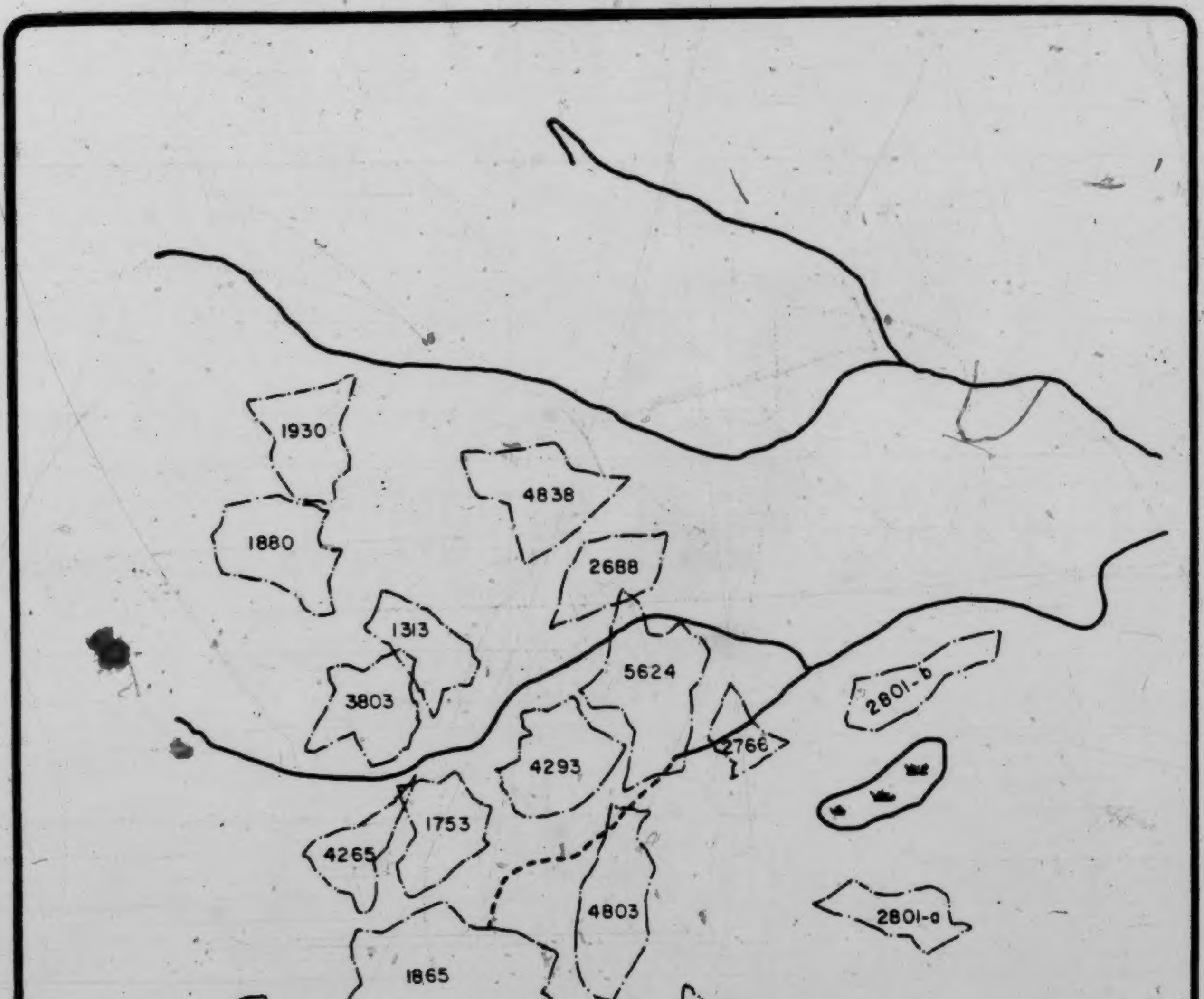
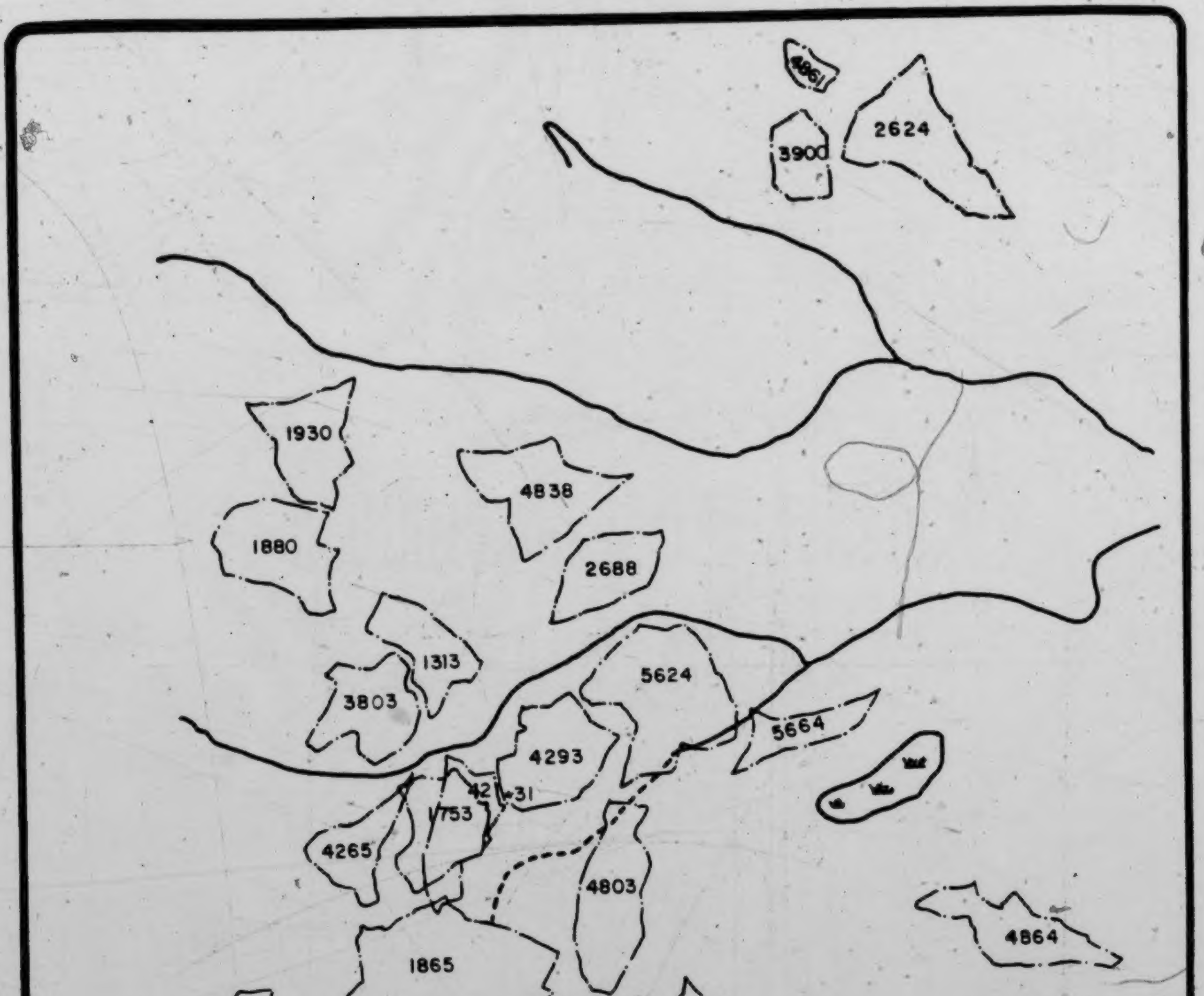

1930
4838
1880
2688
1313
5624
3803
2801-b
2766
4293
1753
4265
4803
2801-a
1865
4838
5679
4055
1754
4817
ub
3950
4910
alder bog
stream
intermittent stream
territory boundary
ub unbanded male

Figure 2. Territorial boundaries of male Blue Grouse studied on Comox Burn in 1973. Males 1753 and 4231 were not present simultaneously (see text). Territories of unbanded birds are approximate.


4861
2624
3900
1930
4838
1880
2688
1313
3803
5624
4293
5664
42
31
1753
4265
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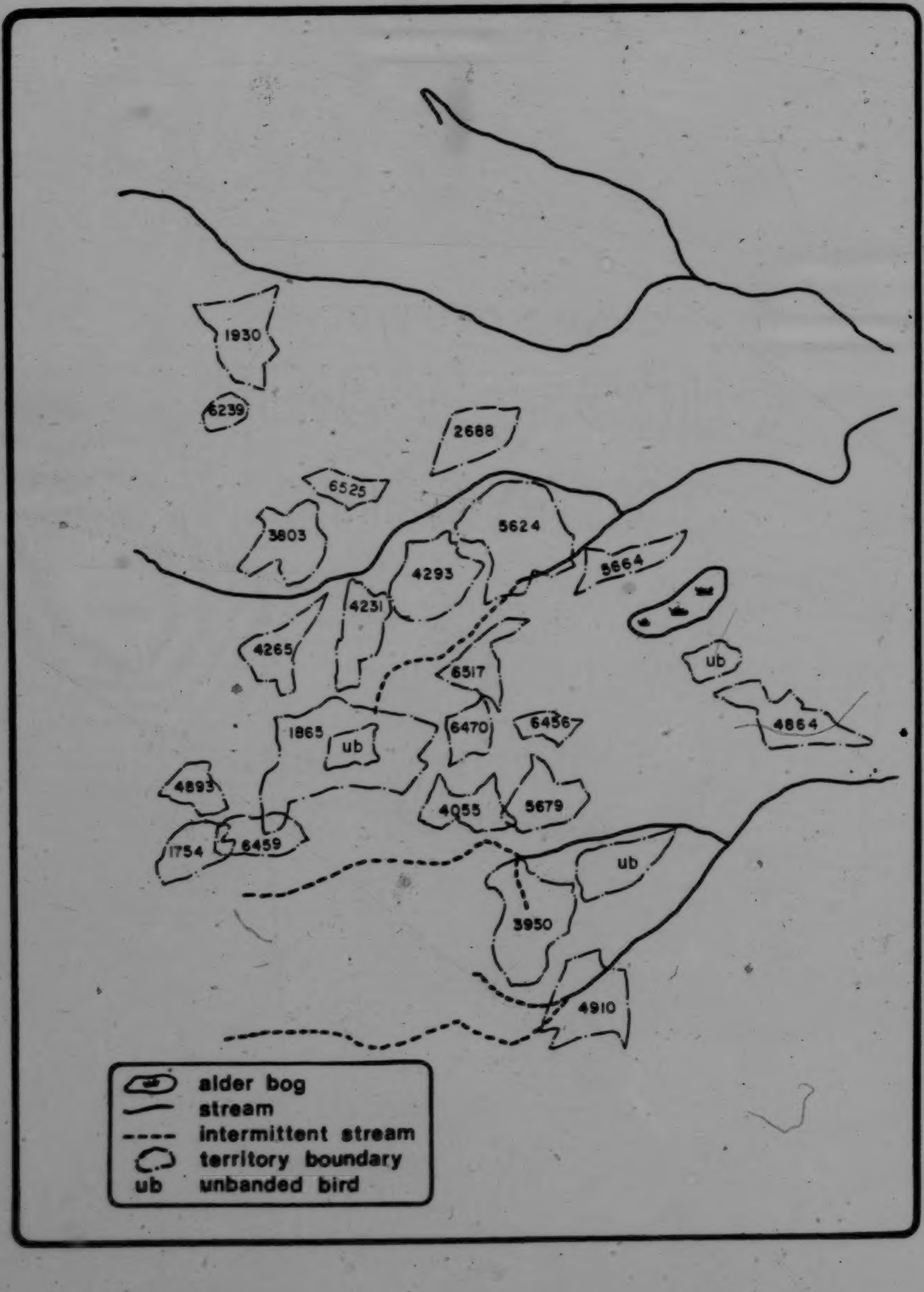
territory boundary
ub unbanded

Figure 3. Territorial boundaries of male Blue Grouse studied in 1974. Boundaries of unbanded birds are approximate. One unbanded bird occupied part of territory of male 1865, while the latter was still present (see text). Territories of unbanded birds and approximate.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LITERATURE CITED

ANDERSON, A.H., & A. ANDERSON. 1973. The Cactus Wren. Tucson, Univ. Arizona Press.

ARMSTRONG, E.A. 1947. Bird display and behaviour: an introduction to the study of bird psychology. Second ed. New York, Dover.

______. 1955. The Wren. London, Collins.

______. 1973. A study of bird song, Second ed. New York, Dover.

BALLARD, W.B., AND R.J. ROBEL. 1974. Reproductive importance of dominant male Greater Prairie Chickens. Auk 91: 75-85.

BEER, J.R., L.D. FRENZEL, & N. HANSEN. 1956. Minimum space requirements of some nesting passerine birds. Wilson Bull. 68:200-209.

BENDELL, J.F. 1955. Age, breeding behavior and migration of Blue Grouse, _Dendgrapus obscurus fuliginosus_ (Ridgway). Can. J. Zool. 33:195-223.

______, & F.W. ELLIOTT. 1966. Habitat selection in Blue Grouse. Condor 68: 431-446.

____________. 1967. Behaviour and the regulation of numbers in Blue Grouse. Can. Wildl. Serv. Rept. Ser. No. 4.

______, D.G. KING, & D.H. MOSSOP. 1972. Removal and repopulation of Blue Grouse in a declining population J. Wildlife Manage. 36: 1153-1165.

BENT, A.C. 1932. Life histories of North American gallinaceous birds. U.S. Natl. Mus. Bull. 126 (Dover reprint 1963).

BERGERUD, A.T., & D.H. HEMUS. 1975. An experimental study of the behavior of Blue Grouse (_Dendragapus obscurus_). I. Differences between the founders from three populations. Can. J. Zool. 53: 1222-1237.

BLACKFORD, J.L. 1958. Territoriality and breeding behavior of a population of Blue Grouse in Montana. Condor 60: 145-158.

______. 1963. Further observations on the breeding behavior of a Blue Grouse population in Montana. Condor 65: 485-513.

BOAG, D.A. 1966. Population attributes of Blue Grouse in southwestern Alberta. Can. J. Zool. 44: 799-513.

______. 1976. Influence of changing grouse density and forest attributes on the occupancy of a series of potential territories by male Ruffed Grouse. Can. J. Zool. 54: 1727-1736.

BROWN, J. & J.M. GREEN. 1976. Territoriality, habitat selection and prior residence in underyearling Stichaeus punctatus (Pisces: Stichaeida). Can. J. Zool. 54: 1904-1907.

CONDER, P.J. 1948. The breeding biology and behavior of the Continental Goldfinch Carduelis carduelis cardauelis. Ibis 90: 493-525.

DONALDSON, J.L. 1973. A behavioral and demographic study of an insular population of Blue Grouse. B.S. thesis, Victoria, Univ. Victoria.

FALLS, J.B., AND M.K. MC NICHOLL. 1978. Neighbor-stranger discrimination by song in male Blue Grouse. in Ph.D. thesis, Univ. Alberta, Edmonton.

HAMERSTROM, F., AND F. HAMERSTROM. 1960. Comparability of some social displays of grouse. Proc. 12th Intern. Ornithol. Congr.: 274-293.

HARJU, H. 1974. An analysis of some aspects of the ecology of Dusky Grouse. Ph.D. thesis, Laramie, Univ. Wyoming.

HARTZLER, J.E. 1972. An analysis of Sage Grouse lek behavior. Ph.D. thesis, Missoula, Univ. Montana.

HINDE, R.A. 1956. The biological significance of the territories of birds. Ibis 98: 340-369.

HJORTH, I. 1970. Reproductive behavior in Tetraonidae with special reference to males. Viltrevy 7: 184-588.

HOFFMAN, R.S. 1956. Observations on a Sooty Grouse population at Sage Hen Creek, California. Condor 58: 321-337.

JOHNSGARD, P.A. 1973. Grouse and quails of North America. Univ. Nebraska Press, Lincoln.

LACK, D. 1965. The life of the Robin. 4th edition. London, H.F. & G. Witherby.

LEYHAUSEN, P. 1971. Dominance and territoriality as complemented in mammalian social structure. pp. 23-33 in ESSER, A.H. (Editor). Behavior and environment. The use of space by animals and men. New York, Plenum Press.

MARTIN, K. 1973. Breeding density and reproductive success of Robins in relation to habitat structure on logged areas of Vancouver Island, British Columbia. M.Sc. thesis, Univ. Alberta, Edmonton.

MARTINKA, R.R. 1972. Structural characteristics of Blue Grouse territories in southwestern Montana. J. Wildlife Manage. 36: 498-510.

MAYR, E. 1935. Bernard Altum and the territory theory. Proc. Linn. Soc. New York 45-46: 1-15.

MCNICHOLL, M.K. 1975. Larid site tenacity and group adherence in relation to habitat. Auk 92: 98-104.

______. 1978a. Vocal communication among Blue Grouse. in Ph.D. thesis, Edmonton, Univ. Alberta.

______. 1978b. Functional aspects of some display components of male Blue Grouse. in Ph.D. thesis, Edmonton, Univ. Alberta.

NICE, M.M. 1941. The role of territory in bird life. Am. Midl. Nat. 26: 441-487.

______. 1943. Studies in the life history of the Song Sparrow. Vol. 2. The behavior of the Song Sparrow and other passerines. Trans. Linnaean Soc. New York. 6.

ODUM, E. P., & E. J. KUENZLER. 1955. Measurement of territory and home range in birds. Auk 72: 128-137.

PITELKA, F.A. 1959. Numbers, breeding schedule, and territoriality of Pectoral Sandpipers of northern Alaska. Condor 61: 233-264.

RIPPIN, A.B., & D.A. BOAG. 1974. Spacial organization among male Sharp-tailed Grouse on arenas. Can. J. Zool. 52: 591-597.

STENGER, J., & J.B. FALLS. 1959. The utilized territory of the Ovenbird. Wilson Bull. 71: 125-140.

THOMPSON, E.E. 1891. The birds of Manitoba. Proc. U.S. Natl. Mus. 13: 457-643.

TRIVERS, R.L. 1972. Parental investment and sexual selection. pp. 136-179 _in_ Campbell, B. (editor). Sexual selection and the descent of man 1871-1971. Chicago, Aldine Publ. Co.

VERNER, J. 1977. On the adaptive significance of territoriality. Am. Nat. 111: 769-775.

WHITNEY, C.L., & J.R. KREBS. 1975. Spacing and calling in Pacific Tree Frogs, _Hyla regilla_. Can. J. Zool. 53: 1519-1527.

WILEY, R.H. 1974. Evolution of social organization and life-history patterns among grouse. Quart. Rev. Biol. 49: 201-226.

WING, L. 1946. Drumming flight in the Blue Grouse and courtship characters of the Tetraonidae. Condor 48: 145-147.

ZAR, J.H. 1974. Biostatistical analysis. Englewood Cliffs, Prentice-Hall.

ZWICKEL, F.C. 1972. Removal and repopulation of Blue Grouse in an increasing population. J. Wildlife Manage. 36: 1141-1152.

ZWICKEL, F.C., & J.F. BENDELL. 1972. Blue Grouse, habitat and populations. Proc. 15th Intern. Ornith. Cong.: 150-169.

THESIS DISCUSSION

SOCIAL ORGANIZATION OF MALE BLUE GROUSE

Although territorial and hierachial systems are often regarded as separate types of social systems (e.g. Wynne-Edwards 1965; Wilson 1975), my data suggest that the social system of male Blue Grouse combines elements of both territory and dominance. In this discussion, I shall summarize features of both lek and solitary territorial systems found in Blue Grouse, then consider factors that favor this combined system.

Male Blue Grouse exhibit at least three, possibly four, characteristics common to lek species (see Armstrong 1964; Hjorth 1970). First, they have bright adornments and an elaborate system of producing sounds (Hjorth 1970; Stirling and Bendell 1970; this study). Secondly, definite hooting groups or associations were apparent in my population. Thirdly, the same population showed some evidence of a form of dominance, in that certain males were dominant over others in singing. Finally, there is some evidence that females approach males to mate, rather than males approaching females. In experiments using recorded female calls, males on territories tended to be very slow in approaching, even though they responded quickly by changes in singing. Thus, males resident on territory tend to wait for the female to approach and only approach her if she is close or does not approach for a considerable period. Although Hjorth (1970) characterized Blue Grouse as a polygamous species with solitary display, their vocal behaviour is socially oriented, and males form distinct social groups during singing.

Unlike lek species, male Blue Grouse rarely congregate at a dancing ground or arena, the territories are not abandoned during parts of the day when the communal display does not take place, and groups of females do not congregate nearby.

Male Blue Grouse appear to occupy territories from which other adult males are excluded, as shown by pattern of dispersion and by aggressive responses to other males (or dummies) within the territory. These are true territories by Pitelka's (1959) definition of "exclusive area." The use of close range cues (visual displays) to establish and maintain territories and longer range cues (song) to help maintain territories is a common feature of territorial birds (Armstrong 1973; Thorpe 1961). Moreover, as with several species of passerines (Falls 1969), males can discriminate between the songs of neighbors in the "correct" direction and those of other individuals.

Thus, Blue Grouse combine features of both territorial and dominance systems, in a system in which males are much more dispersed than in lek species, but still within hearing distance of one another ("exploded arena" of Gilliard 1963). Similar combinations of dominance and territorial systems have been described in other birds (Snow 1963; Anderson and Anderson 1973; Armstrong 1973) and in lizards (Boag 1973).

I suggest that the social system of male Blue Grouse involves territorial birds which sing in distinct social groups. Within these groups, a dominance is present. Females mate only with territorial males, and perhaps mainly with those which dominate others in singing. Yearling males and some younger adults are "surplus" birds which quickly fill in territories of birds which have died. In most cases birds with established territories return in succeeding years and do not occupy new territories (Bendell and Elliott 1967; this study). "Surplus" birds are likely watching for a vacancy and will not challenge the resident unless he appears weak or injured. Although such birds may replace lost residents, they rarely (if ever) occupy territories identical to those of the previous occupants.

One advantage suggested for lek behavior is that females may select males who are genetically the most fit, with dominance being an indication of genetic superiority (Trivers 1972). In such a system the majority of matings are effected by a few dominant males (Hartzler 1972; Wiley 1974, 1978), these occupying central territories (Rippin and Boag 1974), but even these individuals must mate quickly or subordinates interfere (Hartzler 1972; Trivers 1972; Wiley 1978). In a territorial species with singing dominance, such birds could mate without interference if females could select "superior" males with which to mate by detecting male dominance through singing patterns.

A major advantage attributed to lek behavior is that of group stimulation (Armstrong 1964). Snow (1963) pointed out that lekking behavior would be of advantage to males in species with no pair bond if display by the group at close quarters had an attractive and stimulating power more than the combined power of each displaying solitarily. In such situations any advantage in displaying away from rivals would be lost, as each would leave more offspring from the group situation unless predation or some other negative factor outweighed this advantage. However, as Fisher (1954) pointed out, song in territorial birds also has a marked stimulatory effect (e.g. Thorpe 1961; Brockway 1962, 1969; Armstrong 1973). Since Blue Grouse song can be heard for distances exceeding several territories, singing in social groups may serve to increase their attractive and stimulating power without aggregating at communal sites.

A disadvantage of display aggregations is in the increased liklihood that such conspicuous birds gathering together in a predictable spot will be detected by a predator (Armstrong 1964). Blue Grouse neither gather together, nor always sing at one predictable spot, but rather have several hooting posts. Wiley (1974) pointed out that lekking species of grouse are primarily those of open habitats from which predators could usually be detected in plenty of time for escape. He suggested that forest grouse do not form leks because the forest would prevent them from detecting predators in time to escape. In this regard, it is interesting to note that Blue Grouse are forest birds that frequently occupy areas opened by fire or logging (Zwickel and Bendell 1972), and thus at times occupy open areas, and at other times dense forest. If the social stimulation provided by singing groups increases the number of offspring of each male, as suggested by Snow (1963), and if this additional increase was offset by greater predation at aggregations in forests, one might expect that such aggregations would occur at least occasionally in open areas. Claims have been made that communal displays occur in inland races (Wing 1946; Blackford 1958, 1963; Harju 1974), though the extent of this behavior has not been investigated in detail.

Thus, several advantages may accrued to male Blue Grouse in combining dominance (or at least communal) and territorial social systems.

LITERATURE CITED

ANDERSON, A.H., and A. ANDERSON. 1973. The Cactus Wren. Univ. Arizona Press, Tucson.

ARMSTRONG, E.A. 1964. Lek display. pp. 431-433 in THOMSON, A.L. (Editor). A new dictionary of birds. McGraw-Hill, New York.

ARMSTRONG, E.A. 1973. A study of bird song. Second ed., Dover, New York.

BENDELL, J.F., and P.W. ELLIOTT. 1967. Behaviour and the regulation of numbers in Blue Grouse. Can. Wildl. Serv. Rept. ser. No. 4.

BLACKFORD, J.L. 1958. Territoriality and breeding behavior of a population of Blue Grouse in Montana. Condor 60: 145-158.

BLACKFORD, J.L. 1963. Further observations on the breeding behavior of a Blue Grouse population in Montana. Condor 65: 485-513.

BOAG, D.A. 1973. Spatial relationships among members of a population of Wall Lizards. Oecologia 12: 1-13.

BROCKWAY, B.F. 1962. The effects of nest-entrance position and male vocalization on reproduction in Budgerigars. Living Bird 1: 93-101.

BROCKWAY, B.F. 1969. Roles of Budgerigar vocalization in the integration of breeding behaviour. pp. 131-158 in HINDE, R.A. (Editor). Bird vocalizations, their relation to current problems in biology and psychology. Cambridge Univ. Press, Cambridge.

CARRICK, R. 1972. Population ecology of the Australian Black-backed Magpie, Royal Penguin, and Silver Gull. pp. 41-99 in Population ecology of migratory birds. U.S. Bur. Sport Fish. and Wildlife, Wildlife Res. Rept. 2.

FALLS, J.B. 1969. Functions of territorial song in the White-throated Sparrow. pp. 207-232 in HINDE, R.A. (Editor). Bird vocalizations, their relation to current problems in biology and psychology. Cambridge Univ. Press, Cambridge.

FISHER, J. 1954. Evolution and bird sociality. pp. 7-83 in HUXLEY, J., and E.B. FORD (Editors). Evolution as a process. George Allen

& Unwin, London.

GILLIARD, E.T. 1963. The evolution of bowerbirds. Scientific Amer. 209(2): 38-46.

HAMERSTROM, F., and F. HAMERSTROM. 1960. Comparability of some social displays of grouse. Proc. 12th Intern. Ornith. Congr.: 274-293.

HARJU, H. 1974. An analysis of some aspects of the ecology of Dusky Grouse. Ph.D. thesis, Univ. Wyoming, Laramie.

HARTZLER, J.E. 1972. An analysis of Sage Grouse lek behavior. Ph.D. thesis, Univ. Montana, Missoula.

HJORTH, I. 1970. Reproductive behaviour in Tetraonidae with special reference to males. Viltrevy 7: 184-588.

PITELKA, F.A. 1959. Numbers, breeding schedule, and territoriality of Pectoral Sandpipers of northern Alaska. Condor 61: 233-264.

RIPPIN, A.B., and D.A. BOAG. 1974. Spacial organization among male Sharp-tailed Grouse on arenas. Can. J. Zool. 52: 591-597.

SNOW, D.W. 1963. The evolution of manakin displays. Proc. 13th Intern. Ornith. Congr.: 553-561.

STIRLING, I., and J.F. BENDELL. 1970. The reproductive behaviour of Blue Grouse. Syesis 3: 161-171.

THORPE, W.H. 1961. Bird-song. The biology of vocal communication and expression in birds. Cambridge Univ. Press, Cambridge.

TRIVERS, R.L. 1972. Parental investment and sexual selection. pp. 136-177 in CAMPBELL, B. (Editor). Sexual selection and the descent of man 1871-1971. Aldine Publ. Co., Chicago.

WILEY, R.H. 1974. Evolution of social organization and life-history patterns among grouse. Quart. Rev. Biol. 49: 201-226.

WILEY, R.H. 1978. The lek mating system of the Sage Grouse. Scientific Amer. 238: 114-125.

WILSON, E.O. 1975. Sociobiology/the new synthesis. Harvard Univ. Press, Cambridge, Mass.

WING, L. 1946. Drumming flight in the Blue Grouse and courtship characters of the Tetraonidae. Condor 48: 154-157.

WYNNE-EDWARDS, V.C. 1965. Self-regulating systems in populations of animals. Science 147: 1543-1548.

ZWICKEL, F.C., and J.F. BENDELL. 1972. Blue Grouse, habitat, and populations. Proc. 15th Intern. Ornith. Congr.: 150-169.

Appendix 1: Caution needed in use of playbacks to census bird populations.

Vocal response to playbacks of taped bird calls has been used as a method of determining population numbers of several species (e.g. Bohl 1956; Stirling and Bendell 1966; Dow 1970; Braun et al. 1973; Glaun 1974; Bennett 1978; and others). Although several studies have shown such a method to produce results comparable to those obtained by more laborious census techniques, responses to playbacks can distort results in some cases. In a recent example, Springer (1978) showed a distortion in sex ratios in census results from playback experiments with Great Horned Owls (Bubo virginianus). In two sets of results, female owls represented 80 and 100 percent of non-responders, thereby incorrectly increasing the proportion of males in the population.

Seasonal variation in response to playbacks contributes another possible distortion factor. Recently, I studied responses by male Blue Grouse (Dendragapus obscurus) to playbacks of various conspecific calls on Vancouver Island, British Columbia (McNicholl 1978). In these experiments, vocal response to the "whinny" female call (Stirling and Bendell 1966) was negative in March, gradually increased in April, peaked in May, and declined again in June and July (Fig. 1). Responses to male song ("hooting") was also seasonal, with no response in March, response vocally only in mid April, and response both vocally and by aggressive approach in late April and May (Fig. 1). During the period in which response was vocal only, live birds, thought to be yearlings and non-territorial adults, were found singing within the territories of resident males. At this time, such birds responded vocally to the "whinny" call, but at times when hooting would provoke attack by resident males, such birds did not respond vocally except to sing quietly near the playback if the resident male did not arrive. Thus, early in the season (mid to late April) playbacks of "whinny" calls could result in more birds hooting than were resident males in a given area. Results in May would produce figures comparable to the actual number of resident males. Results in early April or late in the season would result in numbers lower than the number of resident males present.

Harju (1974) also found a variable response to the "whinny" in males of an inland race of the Blue Grouse. Similarly, Braun et al. (1973) and Glaun (1974) found seasonal variation in responses to calls of White-tailed Ptarmigan (Lagopus leucurus) and rails respectively.

Thus, playbacks can be very useful in censusing bird populations, but seasonal variation in response must be determined before results of such experiments can be assessed properly.

Literature Cited

Bennett, A.J. 1978. Auditory censusing of Greater Sandhill Cranes. Auk 95: 411-413.

Bohl, W.H. 1956. Experiments in locating wild Chukar Partridges by the use of recorded calls. J. Wildlife Manage. 20: 83-85.

Braun, D.E., R.K. Schmidt, Jr., and G.E. Rogers. 1973. Census of Colorado White-tailed Ptarmigan with tape recorded calls. J. Wildlife Manage. 37: 90-93.

Dow, D.D. 1970. Indexing population densities of the Cardinal with tape-recorded song. Wilson Bull. 82: 83-91.

Glaun, J.F. 1974. Study of breeding rails with recorded calls in north-central Colorado. Wilson Bull. 86: 206-214.

Harju, H. 1974. An analysis of some aspects of the ecology of Dusky Grouse. Ph.D. thesis, Univ. Wyoming, Laramie.

McNicholl, M.K. 1978. Functional aspects of some display components of male Blue Grouse. Paper 2 *in* Ph.D. thesis, Univ. Alberta, Edmonton.

Springer, M.A. 1978. Foot surveys versus owl calling surveys: a comparative study of two Great Horned Owl censusing techniques. Inland Bird Banding News 50: 83-93.

Stirling, I., and J.F. Bendell. 1966. Census of Blue Grouse with recorded calls of a female. J. Wildlife Manage. 30: 184-187.

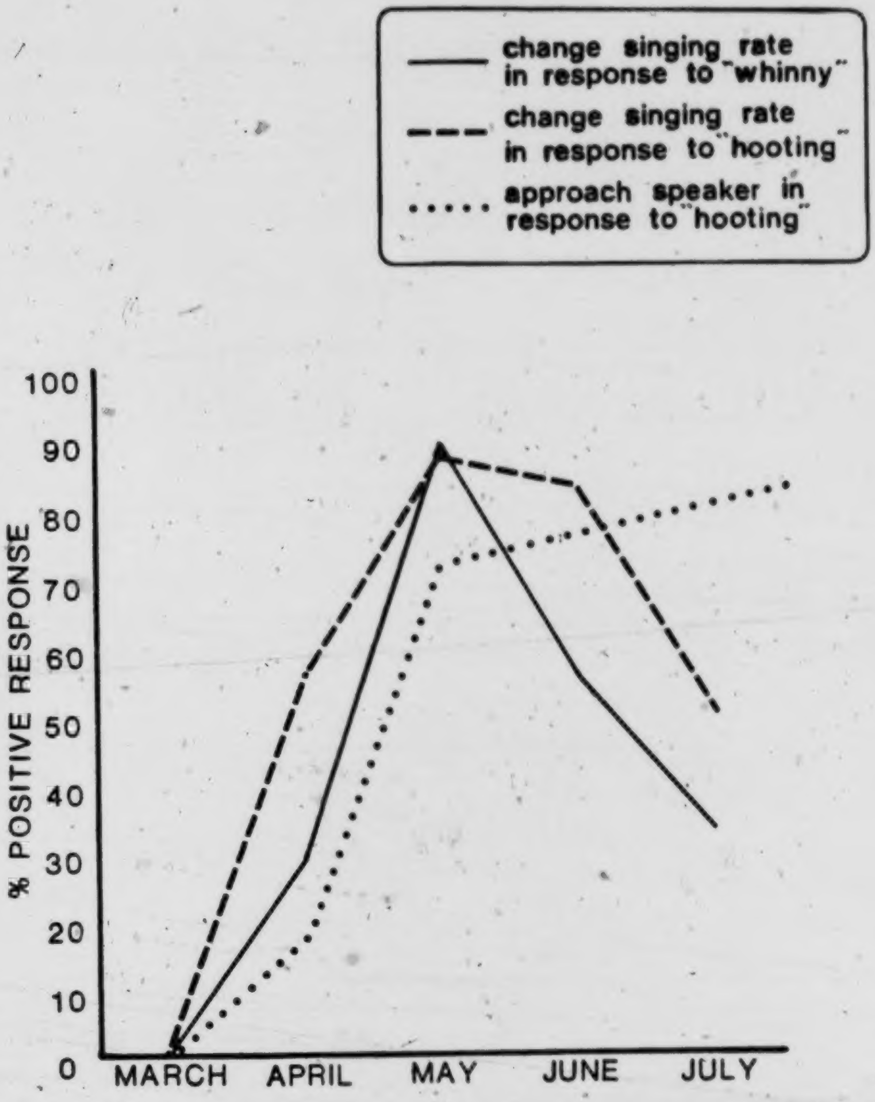

Figure 1 Responses of Male Blue Grouse to Playbacks of the Female "Whinny" and "Hooting" Calls (based on McNicholl 1978: figs. 1 and 2.)

Appendix 2. Reactions of male Blue Grouse to intrusions by observers.

In the summers of 1971 to 1974 I studied social behavior of Blue Grouse (Dendragapus obscurus) on the Comox Burn study area of Vancouver Island (Zwickel 1972). These studies involved both observational and experimental approaches, with approximately 20 males serving as principal subjects each year. Most of these birds (33 of 36 birds studied over the four-year period) were color banded. In experimental situations I identified the subject from a hidden place whenever possible, but if deliberate approach was necessary to confirm the identity, I also recorded the reaction of the bird to me. In addition, I noted reactions of any Blue Grouse males which I encountered accidently.

Table 1 summarizes the reactions of 89 individuals towards me on 474 encounters. I noted a large amount of variability in behavior among individual birds, and in some cases with an individual bird, towards me. Several reactions usually take place on each encounter. For example, a bird that originally crouched may subsequently remain crouched, flush, adopt some form of Alert posture, assume Full Display or a variant of it, or resume Hooting (McNicholl 1978: Table IV).

On nearly 50 percent of the encounters some form of Alert posture was adopted, with Crouches and flushing also frequent (terminology of postures from McNicholl 1978). On the other hand, Aggressive postures, white shoulder-spots, loud landings and Growls seldom occurred. Moreover, these less common responses were apparently characteristic of certain birds (McNicholl unpub. data). Certain "tamer" birds assumed

Full Display or essentially ignored me when I was present. One individual frequently remained Hooting (singing) on one end of a log when I sat down on the other.

Habituation has been suggested as a factor influencing responses to playbacks in several species (e.g. Verner and Milligan 1971). I suggested elsewhere that nesting birds may habituate to the continued presence of a predator, as long as the predator does not attempt to harm the bird or its nest (McNicholl 1973). To test the possibility that male Blue Grouse would similarly habituate to a human observer, I developed a "tameness score" based on features that indicated most wariness through most tameness (Table 2). This is based primarily on behavior after the initial encounter, and thus is behavior exhibited towards me once the bird was able to see me clearly. This classification attempts to avoid effects of the element of surprise. The results indicated that the relative tameness of a given bird remained essentially the same over time (Table 3), rather than showing habituation within a year. Only birds on which ten or more scores were given are included in Table 3. Only three birds (1754, 1865, and 4055) became significantly tamer over time as tested by the Median Test (Siegel 1956), using the Fisher Exact Probability Test or X^2 test for two independent samples (one case only), according to criteria set out by Siegel (1956). Nevertheless, my impression was that most birds became tamer with time, but that these changes were too subtle to be demonstrated in the "tameness" scale. Only one bird (2688) became less tame between years (1972 vs. 1973).

Most reactions towards me were either predator avoidance (Crouch, flush, Alert), or some form of "compromise" posture (Andrew 1956) between tendencies of staying to continue a previous activity and fleeing

(Table 1). Aggression was a rare response, and there are few known cases of aggression towards humans by Blue Grouse (Fisher 1977). For this reason, I doubt that reactions to observers can be used as reliable measures of agonistic behavior by male Blue Grouse, as has been done by some workers (Mossop 1971; Willie 1971; Hemus 1972; Donaldson 1973; Bergerud and Hemus 1975). I found a "standard approach" to birds with which I was very familiar as individuals, and which Hooted in regular, predictable places to be extremely difficult, and I doubt that such a standard approach is realistic in comparing populations. In addition, I do not believe distance of observer prior to flushing or time prior to flushing are valid measures of tameness. Wilder birds tend to either flush at a great distance, or Crouch until the observer is very close, and then flush. Tamer birds flush, if at all, at distances between these extremes.

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Table 1. Reactions of 89 male Blue Grouse to an observer on 474 encounters. For descriptions of postures and display components see McNicholl (1978).

Behavior'	No. occurrences	% of encounters
Neutral	24	5.1
Crouch or variant	144	30.4
Alert or variant	220	46.4
Flush	187	39.5
Full Display or variant	109	23.0
Remain Hooting	67	14.1
Resume Hooting	103	21.7
White Shoulder-spot	11	2.3
Aggressive postures	3	0.6
Growl	34	7.2
Loud landing	32	6.8

' Remain Hooting refers to birds which did not cease to Hoot while I was within sight of them. Most (62) softened the hooting at least briefly. Resume Hooting is used in the case of birds which ran or flushed a short distance and resumed Hooting almost immediately or resumed Hooting at the original spot encountered within sight of me within five min., but does not include those which resumed Hooting in the original spot shortly after my departure from their sight.

Table 2. Tameness score for male Blue Grouse.

Behavior of bird after initial encounter	Score
Flush or run out of sight without resumption of of previous activities.	1
Crouch for extended period; do not resume previous activity within ½ hour; may flush after prolonged Crouch.	2
Flush or run a short distance and resume Hooting.	3
Continue previous activity in view of observer or resume such activity after 5 mins or less.	4
Hoot to and Display towards and/or approach observer.	5

Table 3. Tameness scores for individual male Blue Grouse.

Band	Frequency of each tameness score			P	
				1972	1973
No.	1972	1973	1974	vs.	vs.
	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1973	1974
1754	3 0 0 0 0	5 1 4 0 1	0 0 2 1 0	0.0005*	0.0005*
1865	2 2 3 0 0	3 5 5 0 0	1 3 5 0 0	0.4	0.004*
1930	0 0 3 3 2	0 0 5 2 2	0 0 1 3 2	0.3	0.15
2688	1 2 0 0 0	0 3 0 0 0	1 2 1 0 0	0.05	0.57
3803	0 0 0 0 9	0 0 1 0 9	0 0 0 3 6	0.53	0.53
3950	0 0 1 2 0	0 0 1 4 2	0 0 3 6 1	0.5	0.35
4055	3 5 0 0 0	3 0 2 0 0	0 5 3 0 0	0.3	0.001*
4231	- - - - -	1 2 5 0 0	0 1 4 0 0	-	0.62
4265	1 0 6 0 0	4 2 1 0 0	2 2 6 0 0	0.12	0.13
4293	0 0 5 4 3	0 1 7 5 0	0 1 7 3 0	0.35'	0.52
4803	0 0 1 2 4	0 0 5 0 1	- - - - -	0.04	-
4817	0 1 1 1 1	1 1 3 1 0	- - - - -	0.5	-
4864	- - - - -	0 0 0 2 2	0 0 3 5 0	-	0.25
4893	- - - - -	5 2 0 0 0	5 2 3 0 0	-	0.39
5624	1 4 1 0 0	0 2 5 0 0	1 1 8 5 0	0.37	0.52
5664	- - - - -	4 2 1 0 0	1 2 0 0 0	-	0.42
5670	0 0 1 1 0	0 0 2 0 0	0 0 7 2 0	0.5	0.7
6470	- - - - -	- - - - -	0 3 7 0 0	-	-
6517	- - - - -	0 1 1 0 0	1 1 7 0 0	-	0.82

* significantly different

' by X^2 (others by Fisher Exact Probability Test)

Literature Cited

Andrew, R.J. 1956. Some remarks on behaviour in conflict situations. Brit. J. Anim. Behav. 4:41-45.

Bergerud, A.T. and H.D. Hemus. 1975. An experimental study of the behavior of Blue Grouse (Dendragapus obscurus). I. Differences between the founders from three populations. Can. J. Zool. 53:1222-1237.

Donaldson, J.L. 1973. A behavioral and demographic study of an insular population of Blue Grouse. B.Sc. thesis, Univ. Victoria, Victoria.

Fisher, B.M. 1977. Aggressive behaviour towards humans by a male Blue Grouse. Alberta Nat. 7:232-235.

Hemus, H.D. 1972. A behavioural and demographic comparisons of three Blue Grouse populations released on Moresby Island, B.C. B.Sc. (Hons) thesis, Univ. Victoria, Victoria.

McNicholl, M.K. 1973. Habituation of aggressive responses to avian predators by terns. Auk 90:902-904.

McNicholl, M.K. 1978. Postures and displays of male Blue Grouse. Paper 1 in Ph.D. thesis, Univ. Alberta, Edmonton.

Mossop, D.H. 1971. A relation between aggressive behavior and population dynamics in Blue Grouse. M.Sc. thesis, Univ. British Columbia, Vancouver.

Siegel, S. 1956. Non parametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York.

Verner, J., and M.M. Milligan. 1971. Responses of male White-crowned Sparrows to playback of recorded song. Condor 73:56-64.

Willie, F.B. 1971. Behavior as a possible regulatory mechanism in three Blue Grouse populations on lower Vancouver Island. B.Sc.

thesis, Univ. Victoria, Victoria.

Zwickel, F.C. 1972. Removal and repopulation of Blue Grouse in an increasing population. _J. Wildlife Manage._ 36:1141-1152.

Appendix 3.

TEST OF OBSERVER RELIABILITY ON HOOTING COUNTS

I. 8 May, 1972, Comox Burn gravel pit, with F.C. Zwickel

Minutes from start	Total hoots		Total Whoots		Total birds	
	MKM	FCZ	MKM	FCZ	MKM	FCZ
0-3	55	61	0	0	5+	7
10-13	35	38	0	0	7	5
20-23	37	37	0	0	1	1

II. 9 May, 1972, Middle Quinsam Lake gravel pit, with D. King

Minutes from start	Total hoots		Total Whoots		Total birds	
	MKM	DK	MKM	DK	MKM	DK
0-3	37	39	2	6	3+	3+
10-13	36	40	2	2	5+	5+
20-23	24	24	2	5	4+	3+
30-34	30	30	0	0	3	3

III. 10 May, Middle Quinsam Lake, Consultation Hill, with D.J. Low

Minutes from start	Total hoots		Total Whoots		Total birds	
	MKM	DJL	MKM	DJL	MKM	DJL
0-3	39	42	2	5	3	4
10-13	52	49	0	0	5	4
20-23	28	22	0	1	3	3
30-33	39	33	0	0	3	2

IV. 11 May, Tsolum Main Road, grade 59, with G.F. Searing

Minutes from start	Total hoots		Total Whoots		Total birds	
	MKM	GFS	MKM	GFS	MKM	GFS
0-3	15	8	0	3	1	3
10-13	8	13	8	4	2	5
20-23	28	25	2	3	3	6

(From McNicholl, M.K. 1973. Functions of display components in male Blue Grouse: Progress Report, February 1973. Univ. Alberta, Edmonton. Unpubl. rept.).